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NESTING AND FORAGING BEHAVIOR OF AMERICAN AVOCETS

by

Deborah Arianne Dole

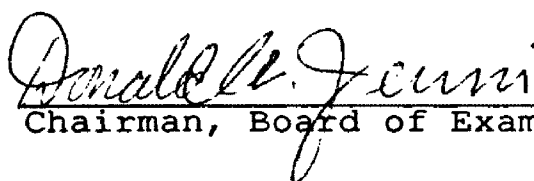
B.A., California State University at Northridge, 1982

Presented in partial fulfillment of the requirements for the  
degree of Master of Arts

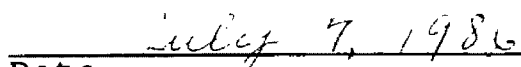
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Dole, Deborah Arianne, M.A., June 1986

Zoology

Nesting and Foraging Behavior of American Avocets (85 pp.)

Director: Donald Jenni *DJ*

American Avocets (Recurvirostra americana) were studied during the 1983 and 1984 breeding seasons in north central Montana. Breeding and foraging activities were documented as were individual differences in nesting behavior and the factors influencing reproductive success.

Breeding occurred from mid-April to mid-August in both years. Laying dates ranged from 30 April to 5 June in 1983 and from 27 April to 12 June in 1984; clutches contained from 1 to 8 eggs. Egg volume ranged from 2.1 cm<sup>3</sup> to 3.8 cm<sup>3</sup> in both years. Distance between nests was highly variable as was nesting habitat; nests were placed on islands, shorelines and dry lake beds, and in areas with bare soil, short grass and tall grass.

Hatching success during both years was high: 71% in 1983 and 79% in 1984. Avocets nesting on shorelines hatched more eggs than others in 1983; those nesting in dry lake beds hatched more eggs than others in 1984. Hatching success also varied with clutch size, laying date, and internest distance.

The tendency of avocets to vary their breeding activities is clearly adaptive. Not only does this tendency allow the birds to compensate for predation by utilizing different anti-predator strategies, but allows survival of at least some nests in times of unexpected weather conditions.

Avocets used five foraging methods: Peck, Plunge, Land/Top Peck, Bill Pursuit, and Scythe. Adults foraged most frequently with Peck and Plunge; chicks with Land/Top Peck. Adults caught more prey at 80-100% leg coverage with Peck and Plunge. Young chicks caught more prey at 00-30% leg coverage with Land/Top Peck. Old chicks foraged most effectively at 40-70% leg coverage with Land/Top Peck.

Avocets at Benton Lake partition their foraging area by depth and by method of foraging thereby minimizing competition between adults and chicks and increasing chances of survival among young. Bill dimorphisms in the adult population may also reduce competition between the sexes.

Avocets have evolved variable breeding strategies and partition foraging areas between age and sex categories. These adaptations probably enhance the ability of avocets to occur in large numbers and maintain high reproductive rates in areas where they coexist with many potential competitors and predators.

## ACKNOWLEDGEMENTS

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## CHAPTER 1

### INTRODUCTION

American Avocets are distinctively marked shorebirds belonging to the family Recurvirostridae. Their slender, upturned bill, their reddish-pink heads during the breeding season, and their distinctively patterned black and white bodies readily identify them. In spring and summer these birds are found throughout the western United States and southern Canada where they feed and nest in alkaline or saline ponds and mudflats (Bent 1927; Palmer 1967; Hamilton 1975). The birds winter along the coast of California and throughout much of Mexico.

All adult avocets are similar in coloration (Bent 1927; Gibson 1971; Hamilton 1975), but the sexes are readily distinguished on the basis of differences in bill shape and size; bills of males are somewhat longer and less recurved than are those of females. In contrast to those of adults, the bills of juvenile avocets are short and straight. These differences in bill morphology and size may allow avocets to partition their food resources, thereby decreasing intraspecific competition. Many methods of partitioning food have been suggested for higher vertebrates, including horizontal or vertical stratification of foraging sites

(Harrison and Buchan 1934; Armstrong 1955; Robins 1971; Gibson 1978), variation in type and size of prey taken (Schoener 1967; Bartholomew 1970; Grant et. al. 1976), and temporal differences in foraging activity (Buckley and Buckley 1974). One of the major purposes of this study was to determine if food resource partitioning exists among different age and sex groups of American Avocets, and if so, how it is accomplished.

Hatching rates of avocets have been reported to be high (Gibson 1971; Sidle and Arnold 1982; but see Sordahl 1980). At Summer Lake Management Area in Oregon avocets hatched 79% of their eggs (Gibson 1971); at Mud Lake in North Dakota 90% of the avocet eggs hatched, whereas at Chase Lake in North Dakota 61% of the eggs did so (Sidle and Arnold 1982). The high hatching success of this species has been attributed principally to lack of predation, often as a result of human intervention in the form of vigorous predator control. A second purpose of this study was to describe the breeding sequence of the American Avocet and to gather quantitative data on hatching success of these birds in an area where there is very little predator control.

To accomplish these goals, both feeding and nesting behavior were studied at Benton Lake National Wildlife Refuge, a refuge that supports a population of approximately 2000 breeding avocets, as well as many potential predators.

Predator control is infrequent and casual, consisting of the occasional elimination of a few California gulls (Larus californicus) and skunks. The study extended over a two year time period, from 15 April to 15 July 1983 and from 28 April to 4 July 1984.

## CHAPTER 2

### STUDY AREA

Observations were made on the Benton Lake National Wildlife Refuge in Cascade and Choteau Counties of north central Montana. Located in a large basin surrounded by gently rolling hills, this alkaline marsh is maintained by pumping water from a nearby creek.

A stipa shortgrass prairie, including numerous species of grasses surrounds the lake. The marsh supports a biotic community composed of many types of soft- and hard- stemmed bulrushes, grasses, and cattails. Early in the breeding season the periphery of the lake consists of several types of areas including: alkali flats without vegetation, expanses of densely packed bulrushes and cattails, densely vegetated areas and areas with loosely dispersed clumps of grass. Alkali flats peripheral to the lake are frequently flooded by severe rainstorms and high winds that push the water ashore. As the water recedes in the spring and summer, most of the area then exposed becomes covered by short grass, and many areas become overgrown by a thick stand of grass up to 2 m in height.

Benton Lake supports a wide variety of shorebirds. In addition to the American Avocet, many species occur in large numbers, including Marbled Godwits (Limosa fedoa), Willets



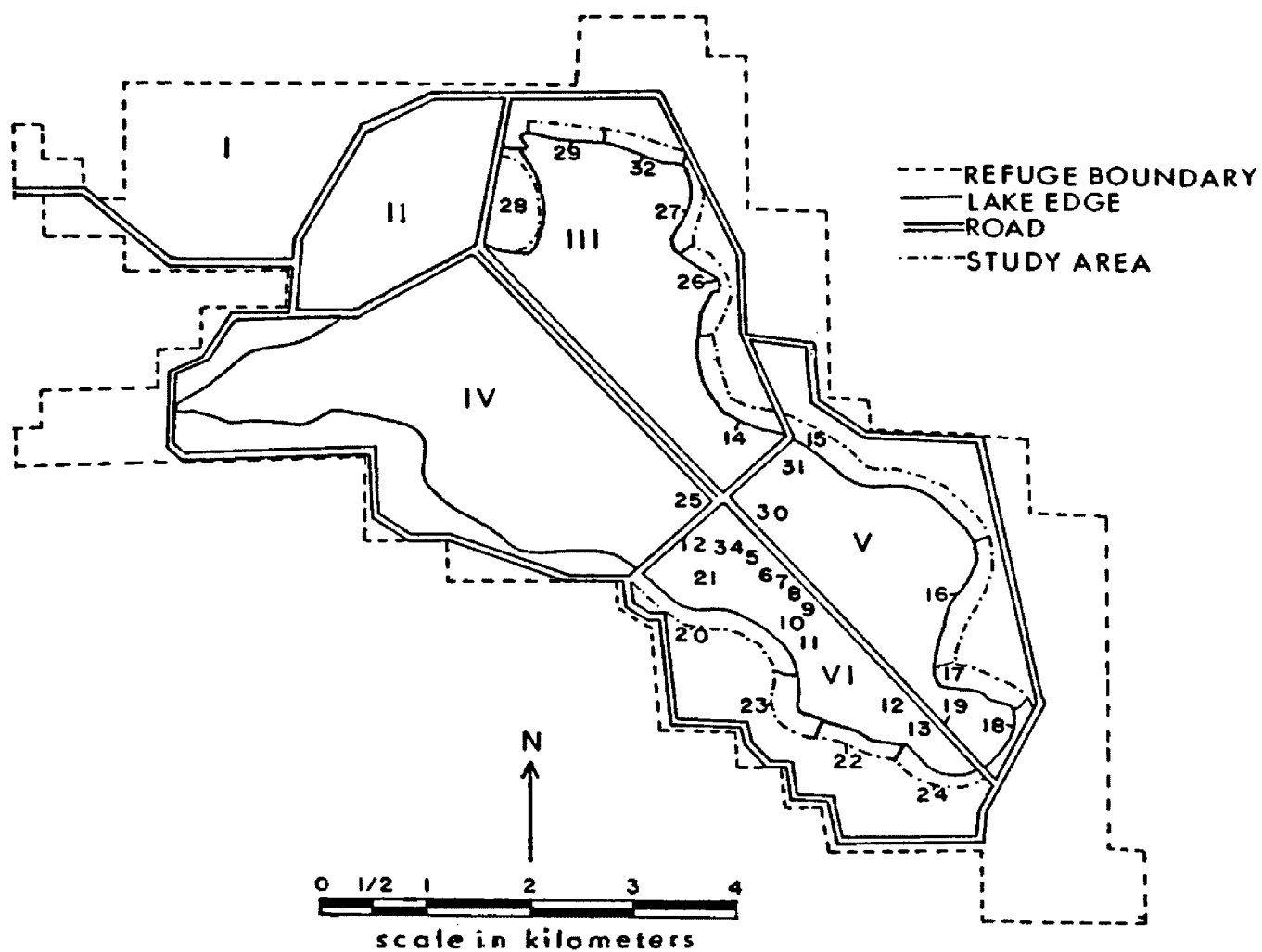
(Catoptrophorus semipalmatus), Wilson's Phalaropes (Phalaropus tricolor), and Killdeer (Charadrius vociferus). Less abundant are: Black-necked Stilts (Himantopus mexicanus), Red-necked Phalaropes (Phalaropus lobatus), Greater Yellowlegs (Tringa melanoleuca) and Mountain Plovers (Charadrius montanus). Still others, Long- and Short-billed Dowitchers (Limnochomus scolopaceus and L. griseus), are migrants but are present in large numbers for three to four weeks as they pass through. Benton Lake also supports many mammals including foxes (Vulpes sp.), badgers (Taxidea taxus), skunks (Mephitis mephitis), raccoons (Procyon lotor), coyotes (Canis latrans) and feral dogs (Canis familiaris).

The spring climate is characterized by occasional, often severe blizzards and hail storms, daily thunderstorms, and frequent winds of 20-40 mph. During June, July, and August it is less windy and daily high temperatures are generally above 25° C.

The marsh is divided into six units separated from each other by dikes (Fig 2-1). The water is maintained at different levels (from "sheet" water of only a few cm to depths of 3 m) in the various units, thereby creating a diversity of feeding habitats. Water levels and conditions in each unit change throughout the year and from year to year. During both years of the study Units I and II were maintained at a depth of 1 to 3 m. During spring and summer of 1983, Unit III was maintained at depths to 3 m, but, in

Fig 2-1. Benton Lake National Wildlife Refuge, Montana.

Roman numerals indicate management units. Smaller numbers and dash-dot lines indicate individual study sites.



1984 it was generally less than 1 m deep. Unit IV was a mud flat covered by only 1 to 5 cm of water during 1983 and by 1984 had dried except for a small section in the center. Unit V, shallow at the beginning of the 1983 season, was subsequently drained completely; the following year it had no water. Unit VI was maintained at a depth of less than 2 m during both years. Units III, IV and VI contained several manmade islands of various sizes.

During 1983 observations were made on birds in and around Units V and VI and the southeastern portions of Units III and IV. Observations in 1984 were restricted to Unit III and the northernmost portion of Unit V.

## CHAPTER 3

### NESTING ACTIVITIES AND HATCHING SUCCESS

In this chapter data are presented that: 1) document the timing of the breeding activities of American Avocets; 2) describe their eggs, nests, and patterns of nest dispersion; 3) quantify hatching success of their eggs; 4) describe the difference among avocets in nesting behaviors; and 5) identify factors that affect the hatching success of the birds.

### METHODS

American Avocets were observed from 15 April to 15 July 1983, and from 28 April to 4 July 1984. The study area was searched on foot each day throughout the first few weeks of each breeding season in order to locate nests. The daily searches enabled me to locate nests as they were established and to check each one regularly during the laying period. Nests found on shorelines were marked by placing a numbered stake 15 paces inland. Those on islands were identified by placing a 5 cm high wooden marker 15 cm from the nest. After incubation began, nests were checked every other day until near hatching, and thereafter were again checked every day.

Eggs in each nest were marked with identifying symbols with a marking pen. When the sequence of laying was known, the eggs were labeled in order. The date each egg was laid (when known), number of eggs in each clutch, and the date on which incubation commenced were recorded for each nest. Length (L) and breadth (B) of each egg were measured using vernier calipers. Egg volume was estimated using the formula  $.00048BL^2$  (Coulson et. al. 1969).

At the onset of incubation various characteristics of the nest site were recorded: height of the nest rim above ground, nature of the nesting material, average height of all cover within 0.3 m of the nest, percent of the nest cup surrounded by some form of vegetative cover, and nature of the substrate and area surrounding the nest. Flooding of the nest or surrounding region was also recorded whenever it occurred.

Eggs about to hatch were identified by one or more characteristics: 1) if date of laying were known, the passage of at least 22 days; 2) a very light and fragile appearance; 3) the occurrence of starring, usually 3-4 days before hatching; 4) beginning of pipping, typically 1 day before hatching.

The hatching date for each egg in each nest was recorded. Wet chicks in nests were assumed to have hatched the day found. Chicks that left the nest without being observed were assumed to have hatched the previous day.

From the above data "nest success", and "egg success" were calculated. Nest success was defined as: the number of nests in which at least one egg hatched, divided by the total number of nests found with eggs. Egg success was defined as: the number of eggs hatching in all nests divided by the total number of eggs.

For each nest, the distance to its nearest neighboring nest and the number of nest within a 35 m radius were recorded. Distances were measured by pacing to the center of each nest.

Behavioral data were collected using binoculars, a spotting scope, and a tape recorder. Most observations were taken from within a vehicle, but in a few cases the observer was clearly visible to the birds. Male and female avocets were distinguished by bill morphology. Sex was confirmed in many cases when birds were seen copulating.

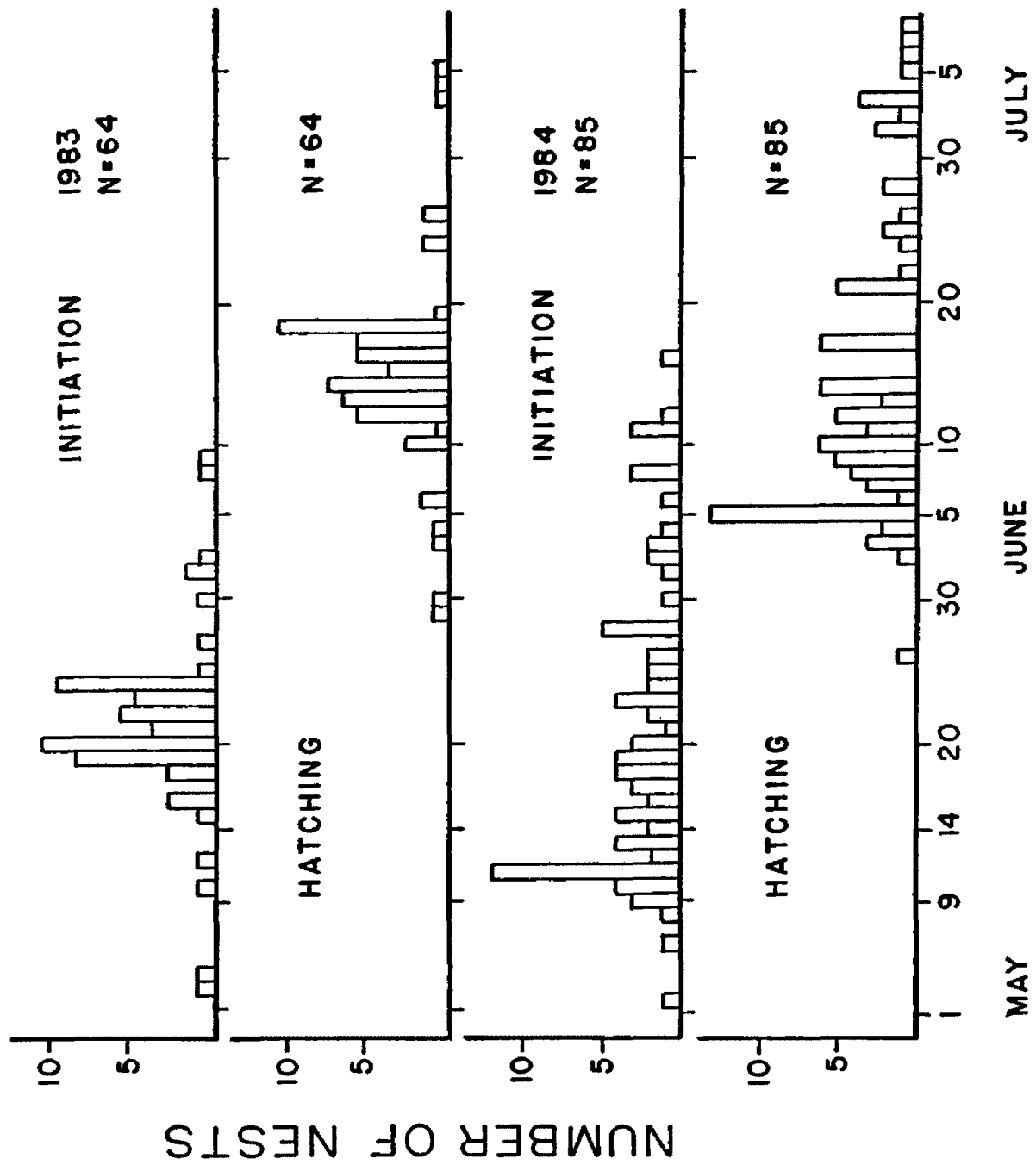
## RESULTS

Breeding activities of avocets in 1983 and 1984 extended over a four month period from mid-April to mid-August (Fig 3-1). Breeding consisted of several stages: pre-laying activities (including courtship, territory establishment, prenest scraping and nest building), laying, incubation, hatching, and brood rearing.

11a

Fig 3-1. Incubation and hatching phenology of American  
Avocets.





### Arrival At The Breeding Grounds

In both years avocets were first seen at Benton Lake by refuge personnel on 14 April. Most arrived by 27 April. Birds arrived in flocks of two to ten individuals but quickly formed into larger foraging flocks, sometimes with as many as 150 birds.

### Territory Establishment

In 1983 territory establishment began about 19 April; territory establishment had already begun when I arrived 28 April 1984. In each year territorial behavior gradually became more and more obvious as increasing numbers of pairs began defending specific areas. Some birds may have arrived already paired (Wolfe 1931; Brown 1948; Gibson 1971; Sordahl 1980), but this could not be documented. Pairs often alternated between territorial behavior and social foraging for several days before becoming strictly territorial.

### Courtship And Mating

Courtship behavior was first observed on 18 April, and the first copulation on 19 April 1983. Copulation had already begun when I arrived 28 April 1984.

Copulation was preceded by a courtship display initiated by either sex that involved a ritualized preening of the breast accompanied by repeated dipping of the bill into the water. Such precopulatory preening by males often became exaggerated and frenzied. As they preened, females, dipped their bills into the water farther and farther away

from the body until both bill and neck were extended along the surface of the water and the posterior portion of the body was slightly raised. This precopulatory posture was held until copulation was completed or aborted; during the precopulatory phase the female adjusted her position so as to keep the male always beside or behind her. After copulation, the pair typically crossed bills and ran together in a circle for two to ten m before separating.

#### Nests And Nest Building

During the prelaying period territorial avocets performed nest scraping activities. Both members of a pair stopped foraging and began running about their territory with their bills held vertically downward, the tips near their feet; while doing this the pair usually remained close together. One of the birds then formed a scrape by placing its breast on the ground, rotating its body, and scratching with its feet. While standing facing away from the scrape the bird then tossed bits of material over its back towards the scrape. Members of a pair often took turns performing these activities. A pair of avocets often made several scrapes before building the final nest.

Avocet nests at Benton Lake were very similar to those described elsewhere (Wetmore 1925; Bent 1927; Wheeler 1955; Gibson 1971; Hamilton 1975; Sordahl 1980; Sidle and Arnold 1982). Usually the nest was little more than a simple scrape on the ground, lined with various amounts of nesting

material such as twigs and dead grasses. Most nests in 1983 (92.4%) and 1984 (74.6%) contained some type of lining material (Table 3-1). The remaining nests were simply depressions in the ground surface or in a clump of grass.

The amount of vegetative material used in nests varied from none to some that contained so much material that they were built up off the ground (Table 3-1). During both 1983 and 1984 fewer than one half of the nests (41.5% and 31.1% respectively) were off the ground.

#### Nest Site

Avocets at Benton Lake nested on islands, shorelines, and dry lake beds. During the 1983 breeding season avocets first began nesting on islands in Unit VI and then on shorelines of other units of the lake. Although the perimeter of Unit VI supported habitats similar to the other shorelines, only two nests were found along the edge of this unit. Units V and III had no islands but many avocets nested on the shorelines of these areas during both years.

Avocets nested in a variety of microhabitats, including bare soil, short grass and tall grass. Most nests were established in open areas where the occupants had an unobstructed view; during 1983, 59.6% and in 1984 71.6% of the nests were in open areas. However, by hatching in 1984 vegetation had grown up around all but 20.0% of the nests. Most (63.2%) were in areas with short or medium height

Table 3-1. Nest characteristics.

Nest characteristics	1983		1984	
	No. of nests	%	No. of nests	%
Depression in ground	56	52.8	18	17.0
Depression in clump of grass	6	5.7	55	51.9
Built off the substrate	44	41.9	33	31.1
Characteristics not recorded	32		8	
Not lined	8	7.6	29	25.4
Lined	97	92.4	85	74.6
With twigs	30	28.6	34	29.8
With grass	60	57.1	29	25.4
With grass and twigs	0	0.0	6	5.3
Slightly lined with twigs	5	4.7	7	6.1
Slightly lined with grass	1	0.9	6	5.3
Built of mud and twigs	1	0.9	3	2.6
Characteristics not recorded	33		0	
No cover around nest cup	65	61.9	63	59.4
Cover around nest cup	40	38.1	43	40.6
Characteristics not recorded	33		8	
Area characteristics during laying				
Bare	62	59.6	68	71.6
Short grass ( < 0.12 m)	13	12.5	12	12.6

Table 3-1. (cont.)

Medium grass (0.13 - 0.37 m)	17	16.3	12	12.6
Tall grass (0.38 - 0.61 m)	12	11.5	3	3.2
Very tall grass ( > 0.61 m)	0	0.0	0	0.0
Characteristics not recorded	34		19	
<hr/>				
Area characteristics at hatch				
Bare	51	49.0	19	20.0
Short grass ( < 0.12 m)	11	10.6	15	15.8
Medium grass (0.13 - 0.37 m)	35	33.7	45	47.4
Tall grass (0.38 - 0.61 m)	7	6.7	6	6.3
Very tall grass ( > 0.61 m)	0	0.0	10	10.5
Characteristics not recorded	34		29	
<hr/>				

vegetation, although 16.8% were in areas with tall or very tall vegetation. During 1983 many (49.0%) nests had no vegetation around them even later in the season.

#### Nest Dispersion

Avocet nests were scattered to varying degrees. During 1983 33.9% of the nests were within 5 m of the nearest other nest, 67.8% were within 15 m of the next nest and 93.3% were within 35 m of the next nest (Fig 3-2). Only 8 nests were solitary, that is, more than 35 m from their nearest neighbor.

In 1984 no nests were within 5 m of the next nest (Fig 3-2). Only 26.0% of the nests were within 15 m of another, 84.4% were within 35 m of the next nest. Nests were solitary 15.6% of the time, far more often than during 1983.

Inter-nest distances along shorelines in 1984 were significantly larger than in 1983 (chi sq. = 31.2,  $p < 0.001$ ,  $df = 9$ ; Fig 3-2). Although nests were dense on islands in 1983, no comparison can be made with 1984 since no measurements were taken on islands in the second year.

The pattern of nest distribution varied depending upon the nature of the area occupied. During 1983 nests on islands (sites 5, 12 and 13) were very tightly clumped; most were within 0-5 m of the nearest neighbor (Table 3-2). On the other hand, nests on shorelines with large expanses of alkali flats (sites 22, 16, 17 and 18), were more widely spaced, averaging between 10 and 20 m apart. Nests on

Fig 3-2. Distances to nearest neighboring nest (A) 1983,  
including islands. (B) 1983, without islands.  
(C) 1984.



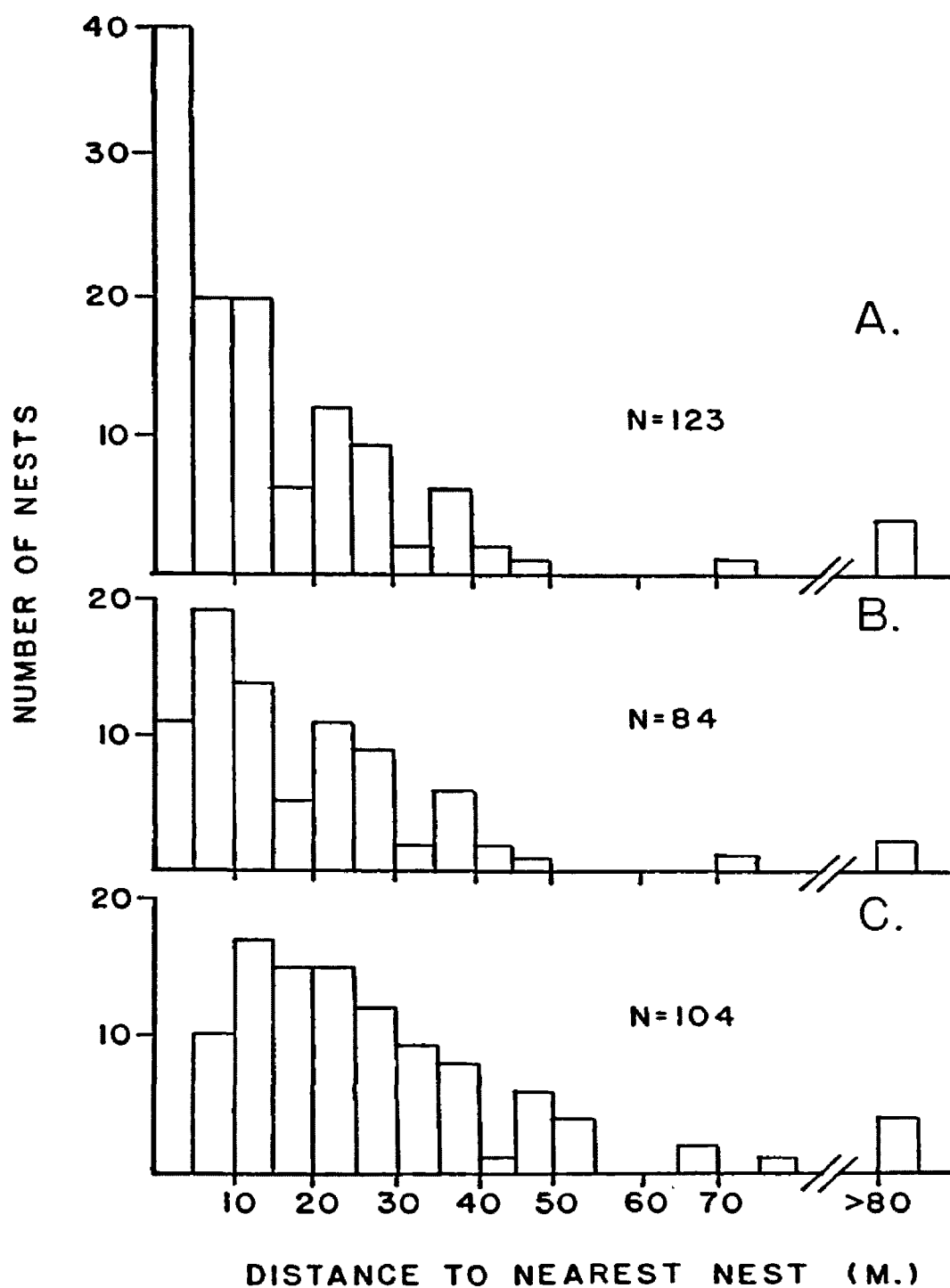


Table 3-2. Average nearest nest distances (NN) (m) for the study sites. -- signifies areas containing two or fewer nests.

Year	Site	Ave. NN distance (m)	Number of nests
1983	1	--	1
	2	--	1
	5	2.5	3
	11	--	1
	12	--	2
	13	3.8	11
	14	22.7	6
1984	14	32.4	3
	26	27.9	5
	27	32.0	7
	28	42.0	8
	29	21.2	31
	30	22.6	28
	31	28.5	16
	32	37.3	4
	33	150.5	3

shorelines supporting only a narrow margin of suitable nesting habitat between the water's edge and the tall dense grass (sites 15 and 14) had the greatest average inter-nest distances, between 20 and 30 m. In 1984 nests in four of the nine regions of the refuge (30, 29, 26, and 31) were within 20-30 m of the next nest. In three sites (27, 14 and 32) the most common inter-nest distances were between 30 and 40 m. In only 2 areas (28 and 33) were nests generally placed more than 40 m away from the nearest nest. Unlike 1983 no clear relationship between the general nature of the areas and inter-nest distances could be discerned during 1984.

#### Egg Laying

The first egg was found on 30 April 1983. On 11 May a severe blizzard that lasted for three days hit Benton Lake and surrounding areas. Most (35 of 43) nests established before the storm were destroyed or abandoned; only eight nests were incubated afterwards. New nests were established several m away from many of the destroyed or abandoned nests and it appeared that avocets were laying replacement clutches. The first egg laid after the storm was found on 15 May. Most egg laying occurred between 15 and 24 May; more avocets laid eggs on 20 and 24 May than on any other day. The last new egg was found on 5 June.

In 1984, the first egg was found on 27 April, three

days earlier than in 1983, and the last newly laid egg was found on 12 June. Most eggs were laid between 4 and 14 May and more avocets laid eggs on 11 May than any other day.

### Clutch Size

Clutch size distributions were significantly different between 1983 and 1984 (chi sq. = 12.8,  $0.01 < p < 0.02$ , df = 4; Fig 3-3). Number of eggs per clutch in 1983 varied from one to eight. In 1983 65% of the nests contained four eggs, 28% contained fewer than 4 eggs and 7% having more than four eggs. In 1984 most (86.8%) of the nests contained four eggs; 13.2% contained fewer. No nests contained more than four eggs.

In both years most clutches of one and two eggs were laid either early or late in the season; very few one-egg clutches were laid in the middle portion of the season. Clutches containing more than five eggs were always laid late in the season. In each nest with more than four eggs, two distinct size classes, shapes, and colors of eggs were present, suggesting that two females had laid eggs in the same nests.

### Egg Size

In 1983, 448 eggs were found after the blizzard; in 1984, 416 eggs were found. Egg volume in both years varied between 2.1 and 3.8 cm<sup>3</sup>, with a mode of 3.0 cm<sup>3</sup> (Fig 3-4). For purposes of analysis eggs were divided into three categories: large (the largest 25%), medium (the 50% of

22a

Fig 3-3. Frequency distribution of clutch sizes.

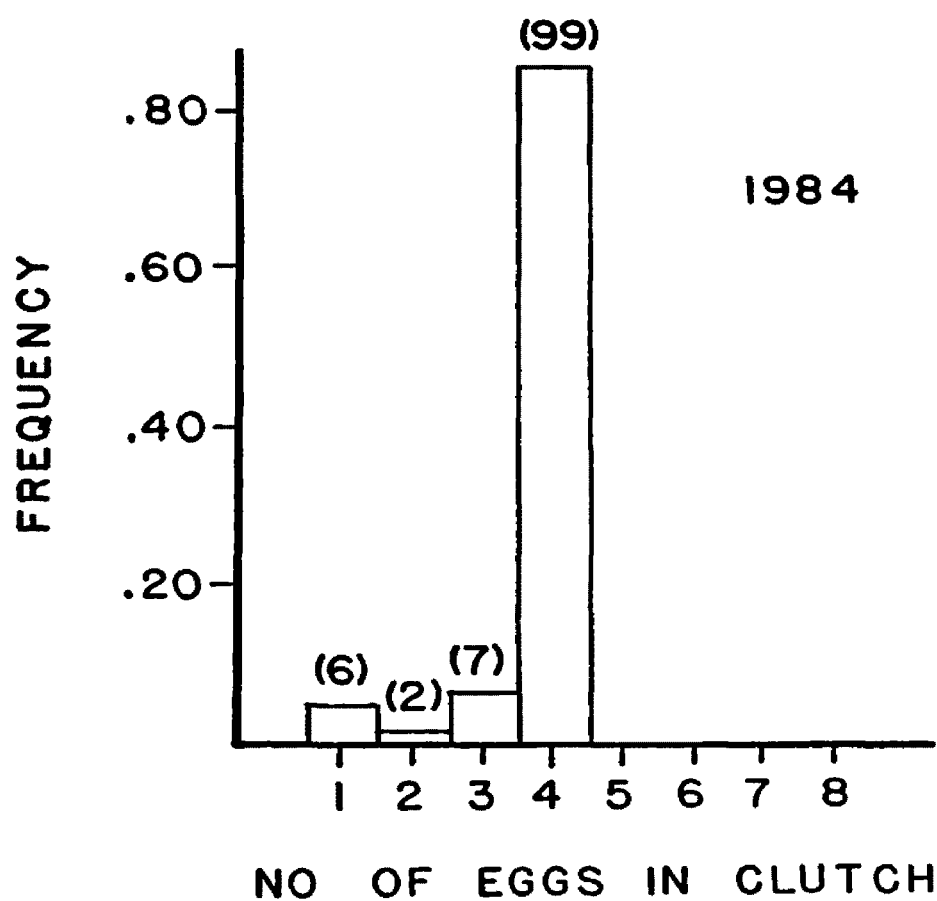
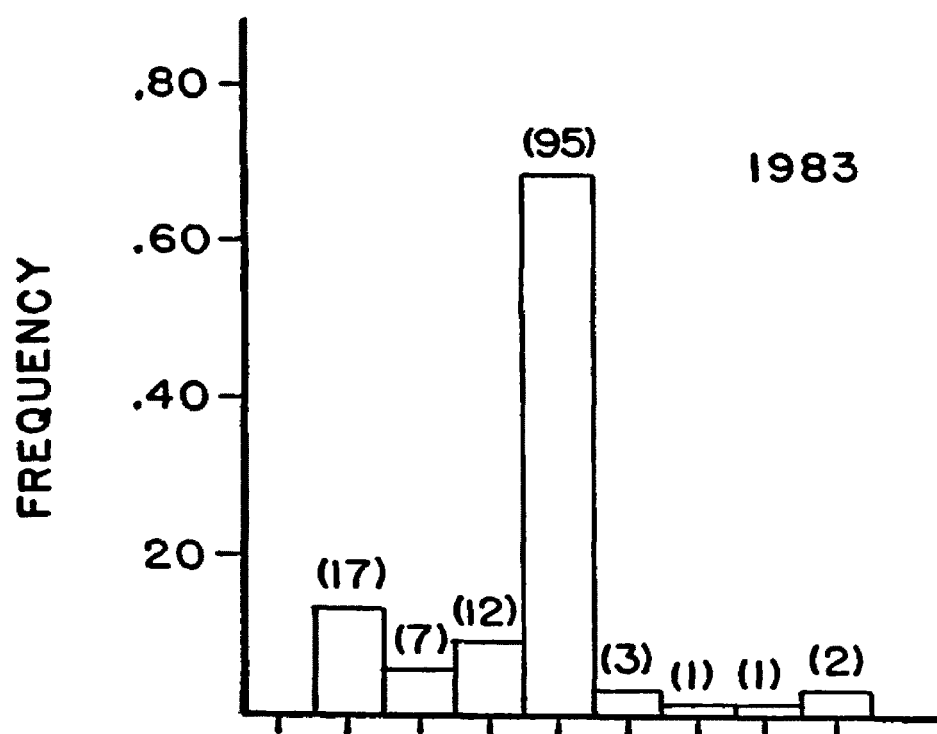
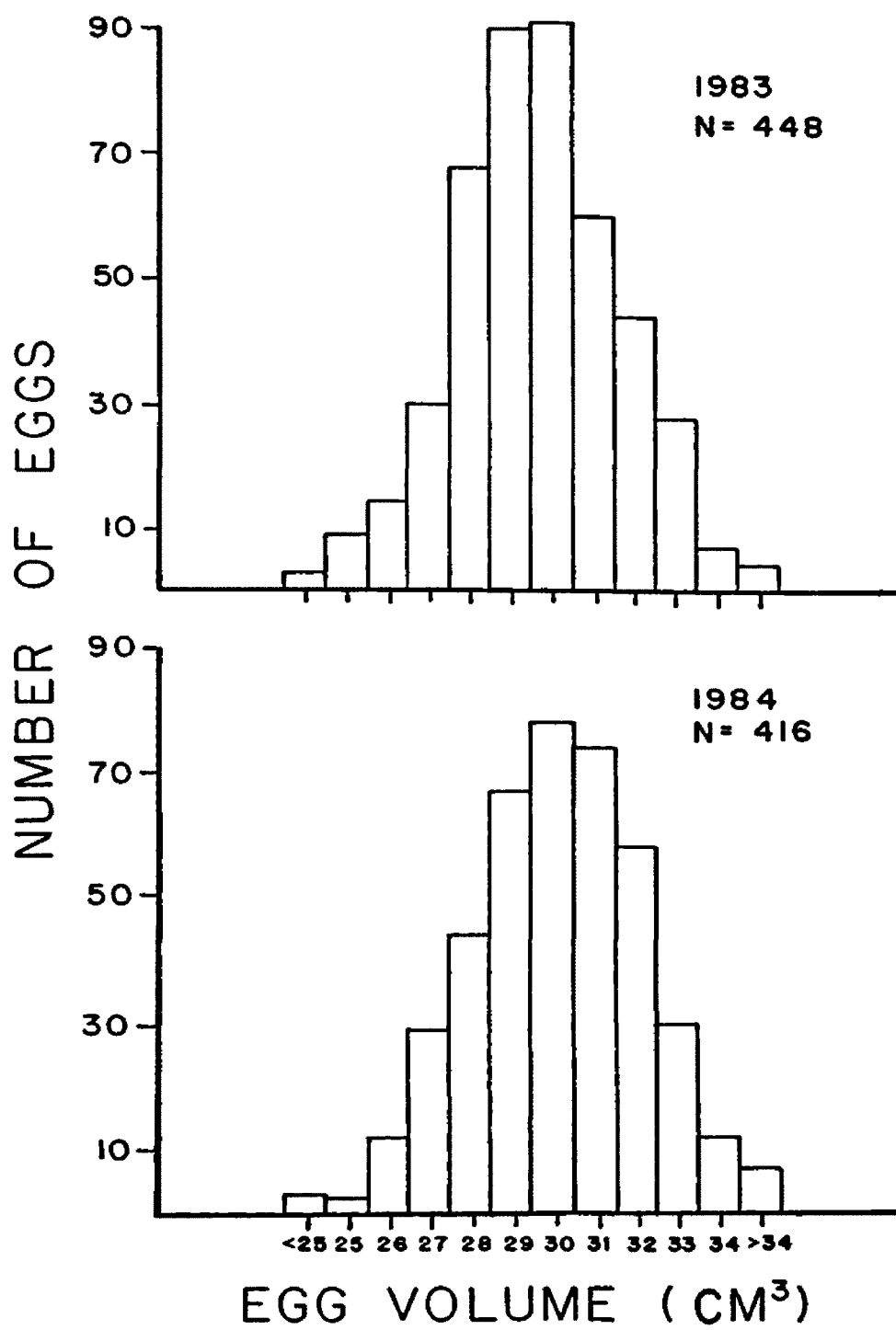


Fig 3-4. Frequency distribution of egg volumes.





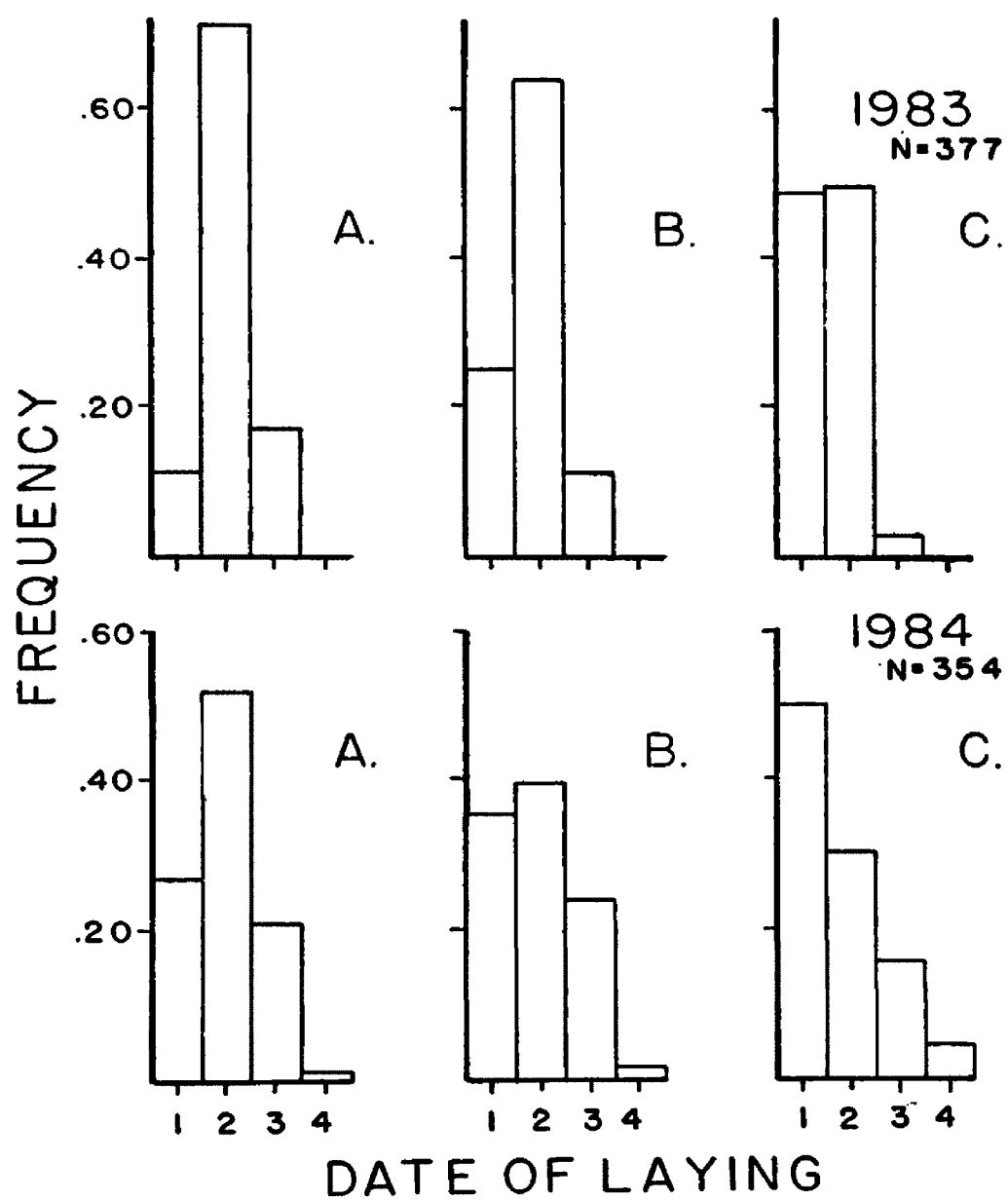
intermediate size) and small (the smallest 25%). Laying dates for small and medium sized eggs did not differ significantly (small/medium:  $\chi^2 = 3.6$ ,  $p > 0.05$ ,  $df = 3$ ), however laying dates for both sizes were significantly different from those of large eggs (small/large:  $\chi^2 = 12.9$ ,  $p < 0.001$ ,  $df = 3$ ; medium/large:  $\chi^2 = 8.7$ ,  $p < 0.05$ ,  $df = 3$ ). Large eggs were laid mainly early in the season, small and medium sized eggs throughout the season (Fig 3-5).

#### Incubation And Nest Attendance

Incubation generally began when the last egg was laid but some birds incubated incomplete clutches during rain storms and in cold weather. Both adults participated in incubation and tended to trade off during the day (Hamilton 1975; Gibson 1971). The incubation period, the interval between the laying and hatching of the last egg, varied from 21 to 27 days; most eggs took 24 days to hatch ( $\bar{X} = 24.3$ ,  $S.D. = 0.917$ ,  $n = 90$ ).

During 1983, avocets were first seen incubating on 4 May and the last date on which incubation was known to have been initiated was 9 June (Fig 3-1); most (75%) avocets began incubating between 19 and 24 May. During 1984, avocets began incubating on 2 May and the last avocet was seen to initiate incubation on 16 June; more than half the birds (50.5%) initiated incubation between 9 and 19 May.

Fig 3-5. Frequency of small, medium and large eggs laid in four time periods. (A) small eggs; (B) medium eggs; (C) large eggs. (1) May 2-15; (2) May 16-29; (3) May 30-June 12; (4) June 13 or later.



## Hatching

Eggs in each clutch usually hatched over a one or two day period. The precocial young were out of the nest within three hours of hatching. Adults removed the egg shells from the nest within one hour of hatching.

Hatching began on 29 May 1983 and 26 May 1984, and continued until 5 and 10 July in the two years respectively. In 1983 the majority (72%) of the eggs hatched from 12 to 18 June (Fig 3-1). In 1984 most eggs (55%) hatched from 3 to 12 June. In the first year more eggs hatched on 18 June than on any other day, whereas in the second more eggs hatched on 5 June than on any other day.

During the first season, nest-success of 138 pairs of breeding avocets was 58%; during 1984, when there was no major blizzard nest-success of 114 breeding pairs was significantly higher, 79% (chi sq. = 3.9,  $p < 0.05$ ,  $df = 1$ ). However, if nests built before the storm in 1983 are excluded, and it is assumed that most of the birds that lost a clutch during the blizzard renested, nest-success in 1983 was 71.4%, and there is no difference between years (chi sq. = 0.21,  $p < 0.05$ ,  $df = 1$ ). Similarly overall egg-success for the two years (54.5% in 1983 and 77% in 1984) were significantly different from each other (chi sq. = 12.2,  $p < 0.001$ ,  $df = 1$ ) when all eggs are included. However,

excluding eggs laid before the storm, egg-success in 1983 and 1984 (75.3% and 77%) are not significantly different ( $\chi^2 = 0.01$ ,  $p > 0.05$ ,  $df = 1$ ).

Significantly more nests lost some or all eggs ( $\chi^2 = 12.5$ ,  $p < 0.001$ ,  $df = 1$ ; Table 3-3) in 1983 than in 1984; in large part due to inclement weather. In addition, more clutches were abandoned, more eggs failed to hatch and more incomplete clutches were laid in 1983 than in 1984. On the other hand, although predation on active nests at which adults were attending was uncommon during both years, predation on active nests occurred more frequently during the 1984 breeding season.

#### Factors Affecting Hatching Success

Egg-success varied with the type of habitat in which the birds placed their nest. In 1983, egg-success ranged from 43.4% (on an island) to 87.5% (on a shoreline) and in 1984 both the highest (90.0%) and lowest (58.3%) egg-success occurred on shorelines (Table 3-4). During the 1983 breeding season, egg-success on islands was 54%, significantly lower ( $\chi^2 = 7.9$ ,  $0.001 < p < 0.01$ ,  $df = 1$ ) than that of birds nesting on shorelines (69.6%). In 1984, egg-success among nests in the dry lake bed (85%) was significantly higher ( $\chi^2 = 13.8$ ,  $p < 0.001$ ,  $df = 1$ ) than among nests on shorelines (68%). In 1984 egg-success in the northeast mudflat was 68%, whereas in the southeast dry lake basin, it was 85.5%; the difference was statistically

Table 3-3. Number of nests in which all or some eggs were lost.

Cause	1983		1984	
	No. of nests	%	No. of nests	%
Weather	35	25.4	8	7.0
Abandoned	9	6.5	0	0.0
Incomplete clutches	22	15.9	2	1.7
Depredated-completely	1	0.7	4	3.5
Depredated-partially	5	3.6	10	8.8
Containing dead/ infertile eggs	16	11.6	7	6.1
Number of nests lost	88	63.8	31	27.2
TOTAL number of nests	138		114	

Table 3-4. Hatching success of American Avocets.

Year	Site	No. of nests hatched/No. of nests	% hatched	No. of eggs hatched/No. of eggs	% hatched
1983					
	5	3/ 7	42.8	10/ 23	43.4
	11	1/ 1	100.0	4/ 4	100.0
	12	2/ 2	100.0	8/ 8	100.0
	13	7/11	63.6	27/ 39	69.2
	14	4/ 6	66.6	17/ 20	85.0
	15	13/21	61.9	47/ 70	67.1
	16	16/21	76.1	62/ 77	80.5
	17	15/17	88.2	56/ 64	87.5
	18	14/27	51.8	54/103	52.4
	19	1/ 1	100.0	4/ 4	100.0
	20	2/ 2	100.0	8/ 8	100.0
	21	7/16	43.7	24/ 49	49.0
	22	4/ 4	100.0	15/ 15	100.0

Table 3-4. (cont.)

1984

14	2/ 3	66.6	7/ 12	58.3
26	5/ 5	100.0	18/ 20	90.0
27	4/ 7	57.1	12/ 20	60.0
28	7/ 8	87.5	25/ 30	83.3
29	22/31	71.0	77/120	64.2
30	24/28	85.7	94/108	87.0
31	13/16	81.3	48/ 58	82.8
32	4/ 4	100.0	14/ 15	93.3



significant (chi sq. = 13.8,  $p < 0.001$ ,  $df = 1$ ). Nest-success rates were not significantly different in the two areas, 74% and 84% for the northeast and southeast areas respectively (chi sq. = 1.2,  $p > 0.05$ ,  $df = 1$ ).

Nest-success varied significantly with clutch size (chi sq. = 59.9,  $p < 0.001$ ,  $df = 2$ ; Fig 3-6); 85.4% of the four-egg clutches in both years produced at least one hatchling, whereas 80% of the three egg nests did so. Clutches of other sizes rarely produced a hatchling (10%).

Predation rates did not vary significantly with egg size in either year (1983: chi sq. = 5.4,  $0.05 < p < 0.10$ ,  $df = 2$ ; 1984: chi sq. = 4.7,  $0.05 < p < 0.10$ ,  $df = 2$ ; Table 3-5). Small, medium, and large eggs were predated in proportion to numbers present in the population. However, nest-success varied with laying date (Fig 3-7).

For successful breeders the mean beginning date of laying in 1983 was 15 May, for partially successful breeders, 17 May, and for unsuccessful breeders, 24 May. These laying dates are significantly different from each other when tested with the Kruskal-Wallis one-way analysis of variance ( $H = 134.9$ ,  $p < 0.001$ ,  $df = 2$ ). In 1984 both successful and partially successful breeders had a mean beginning date of laying of 20 May whereas the mean beginning date of laying for unsuccessful breeders was 23 May, a statistically insignificant difference ( $H = 0.77$ ,  $p > 0.05$ ,  $df = 2$ ).

Fig 3-6. Number of nests with different clutch sizes for three groups of avocets. (A) successful breeders; (B) partially successful breeders; (C) unsuccessful breeders.

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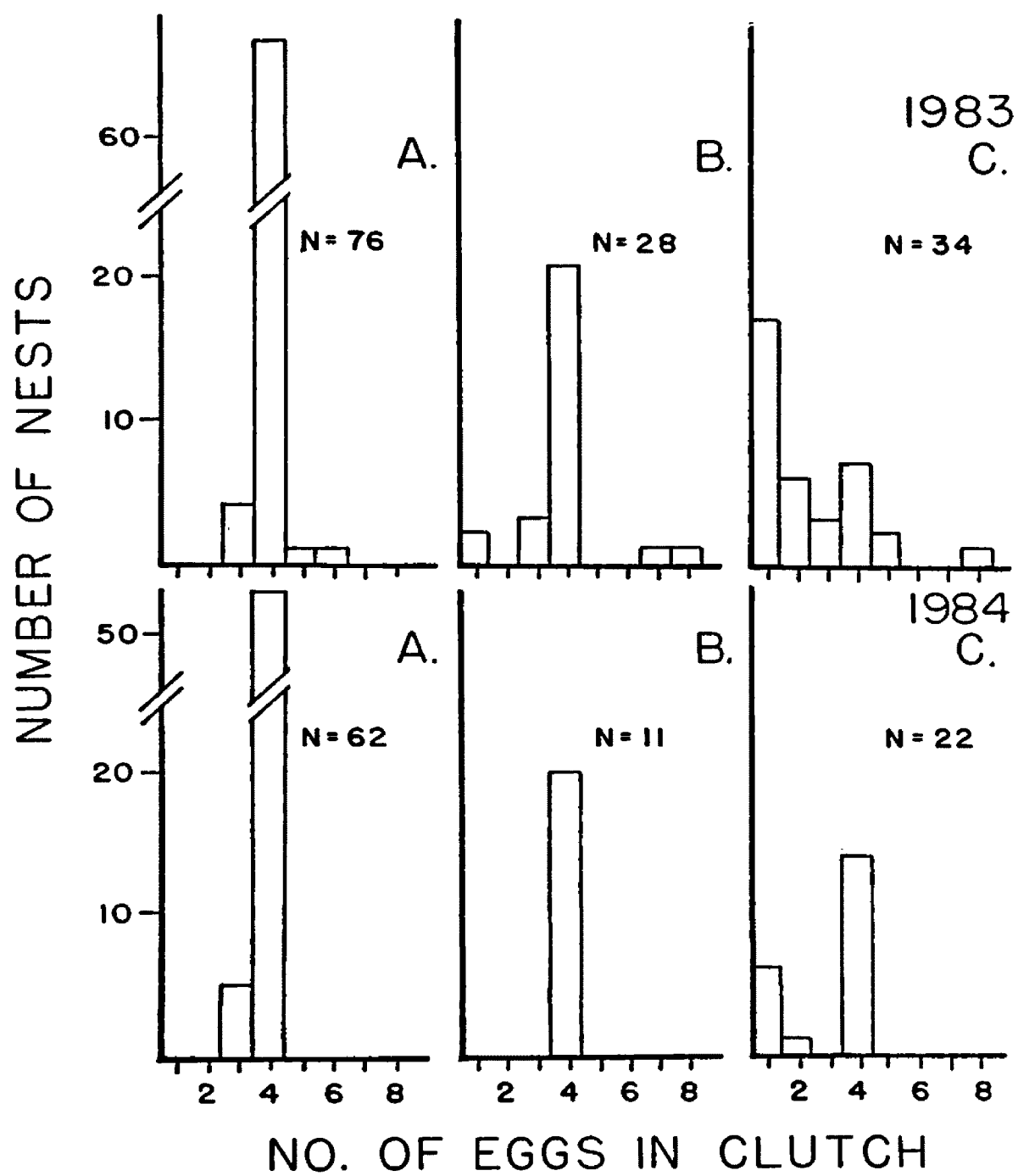
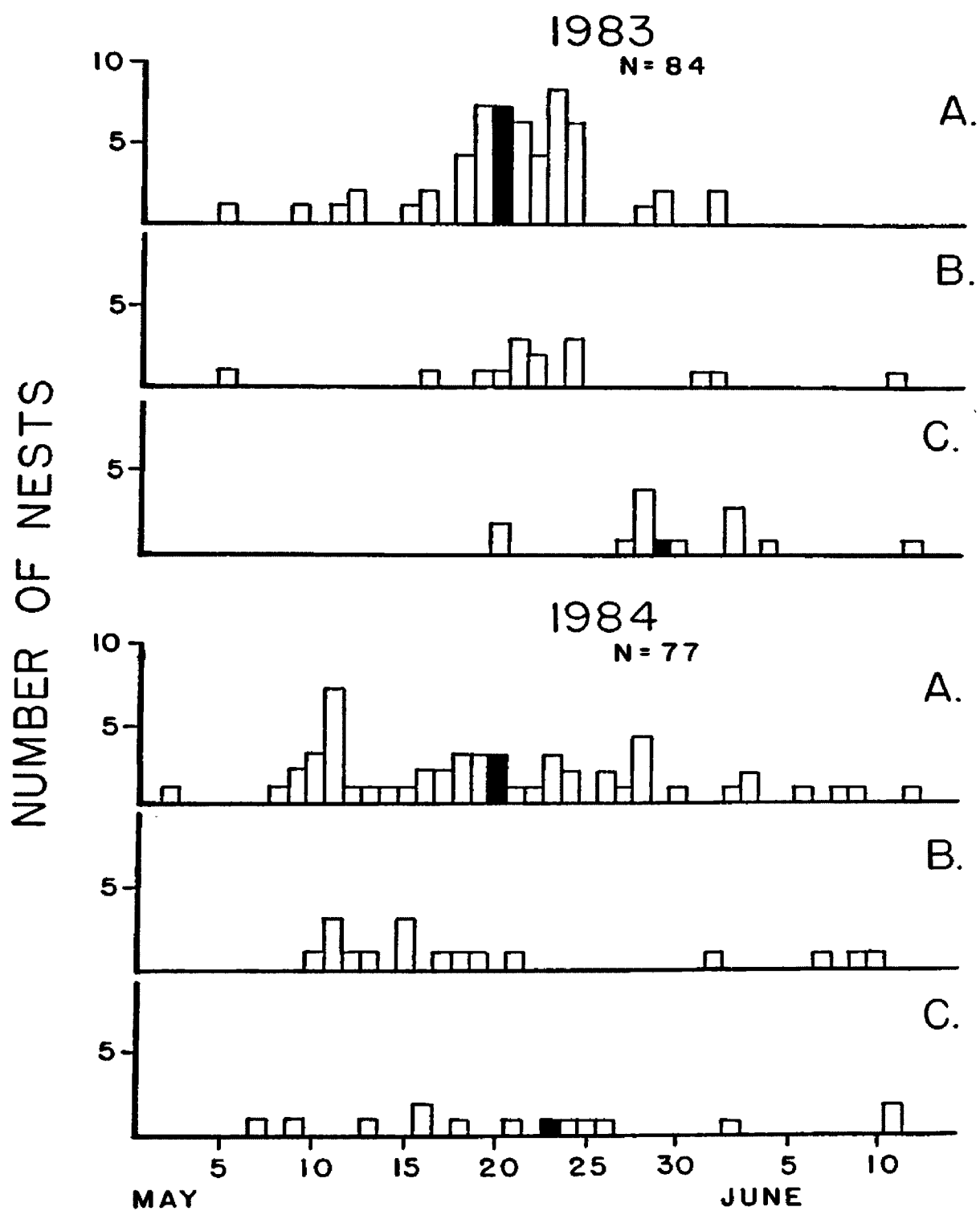


Table 3-5. Size distribution of eggs in the entire population and eggs lost to predators.

Year	Size of egg	Entire population		Depredated	
		No. of eggs	% of total	No. of eggs	% of depredated eggs
1983					
	Large	51	17.3	8	32.0
	Medium	152	51.5	13	52.0
	Small	92	31.2	4	16.0
	TOTAL	295		25	
1984					
	Large	90	25.7	21	21.0
	Medium	185	52.8	62	62.0
	Small	75	21.4	17	17.0
	TOTAL	350		100	

Fig 3-7. Distribution of incubation initiation dates compared among three groups of avocets. (A) successful breeders; (B) partially successful breeders; (C) unsuccessful breeders. Darkened boxes are means.



Egg-success of individual nests did not differ significantly with distance to nearest nest, in either year (Mann-Whitney U 1983: unsuccessful by successful breeders  $U = 1220.5$ ,  $p = 0.06$ ; 1984: unsuccessful by successful breeders  $U = 465.0$ ,  $p = 0.46$ ; Table 3-6). In 1983, successful breeders tended to place their nests farther away from their neighbors than did partially successful breeders who, in turn, placed their nests farther away than did unsuccessful breeders. The average nearest-nest-distance for successful breeders in 1983 was 20.0 m, for partially successful breeders, 16.3 m and for unsuccessful breeders, 14.2 m. Comparable distances in 1984 were 28.2 m, 25.3 m and 30.5 m, respectively. When data for the two years are combined, average nearest-nest-distance was 24.0 m for successful breeders, 21.6 m, for partially successful breeders and 19.5 m for unsuccessful breeders.

#### DISCUSSION

Breeding activity was greatly affected in 1983 by the blizzard that destroyed most early nests and delayed nesting for several weeks. However, many of those that lost clutches in the blizzard appeared to have laid a replacement clutch later in the season. Re-nesting of avocets has also been reported by Sordahl (1980).

The greater variability in clutch size in 1983 may have been due to the effects of the blizzard. Energetic stress

Table 3-6. Mean nearest nest distance (NN) (m) for three categories of breeders.

	Successful		Partially successful		Unsuccessful	
	Ave. NN (m)	No. of nests	Ave. NN (m)	No. of nests	Ave. NN (m)	No. of nests
1983 islands	8.6	14	2.3	5	2.2	11
shorelines	21.2	52	21.2	8	17.8	20
Total	20.0	66	16.1	13	14.2	31
1984*	28.2	61	25.3	19	30.5	15
1983 and 1984	24.0	127	21.6	32	19.5	46

\*1984 data included shorelines only.



to some birds may have caused them to lay one- or two-egg clutches when they re-nested. Additionally, the storm may have occurred when clutches already initiated were incomplete. Because the abnormally large clutches with six-, seven- and eight-eggs contained eggs of two distinct sizes, shapes and colors, it is likely that two females laid in the same nest. The fact that such nests were not seen before the blizzard or in 1984 suggests a relationship to the extreme environmental conditions. Eight-egg nests have been reported previously in avocets (Wolfe 1931; Gibson 1971), but no detailed data about the conditions associated with such nests are available.

Closer placement of nests after the 1983 blizzard may have occurred in part because at the time of re-nesting, much of the nesting area was still flooded or under snow, leaving only a small area suitable for nesting. With a larger than normal proportion of the population (first time nesters plus renesters) laying eggs simultaneously, a closer packing of the nests appears inevitable. Although it is possible that nest density and placement differences between the two years were unrelated to the blizzard and instead due to variations in nesting area suitability within and between areas and years, I believe this is unlikely.

Avocets often were observed building up their nests during storms and flooding. As a result, nests in frequently flooded areas generally were higher than nests in

other areas. A similar build up of nests by avocets during storms or flooding also has been recorded by others (Wetmore 1925; Makkink 1936; Palmer 1967). Avocet nests up to 40 cm high have been recorded in areas subject to flooding (Wetmore 1925).

Avocets that initiated nesting in the middle of the breeding season were more successful on average than were those that began nesting early or late in the season. Early nesters ran the risk of having their clutches destroyed by weather whereas birds nesting late in the season were more frequently subjected to predation. Similarly, the greater hatching success associated with four-egg clutches is the result of at least two opposing factors. Very small clutches apparently did not sufficiently stimulate the incubating "drive" in the bird. At the opposite extreme, it appeared to be physically impossible for one avocet to adequately incubate a very large clutch.

Birds nesting the farthest away from their neighbors hatched more eggs than those nesting closer together. Distribution of nests may in part be a compromise between camouflage and ease of protection from predators. Nests placed far from each other may be difficult for predators to locate, but such nests do not benefit from the assistance of others in predator defense. Closely placed nests may be easier to locate; further, the closeness of the nest virtually assures that once one is located, others are easy

to find also. The presence of several neighbors to assist in predator defense may offset this disadvantage, however at Benton Lake, it did not appear to have done so.

The type of habitat in which a nest is placed is very important to hatching success. During 1983, birds nesting on shorelines hatched more eggs than birds nesting on islands, largely because of high egg loss on islands due to predation. Because the islands at Benton Lake were very small and near shore, mammalian predators may have waded or swum to them and once there easily located eggs among the densely packed nests unconcealed by cover. Island nesting, however, does not always lead to greater predation. Avocets nesting on an island at Mud Lake, North Dakota, experienced no predation. This island however, was about 0.3 km long and equally as far from the shore so that mammalian predators apparently were unable to reach it (Sidle and Arnold 1982).

During 1984 birds nesting on dry lake beds hatched more eggs than those nesting in other habitats. In such areas the nests were fairly far apart and avocet feeding areas were very close by. Although California Gulls often flew over this area, the avocets were constantly vigilant and continually harassed them thereby making it difficult for the gulls to enter the nest area and eat their eggs.

Predation was most common among nests along the northeast shoreline. Not only was this nesting area far

away from the feeding sites so that the avocets could not watch their nests closely while feeding, but the nests were close together and partially screened from each other by scattered clumps of grass. In addition, the entire nesting area was surrounded by a thick stand of bulrushes, perhaps allowing predators to remain concealed until very close to the nests. Once in the nest area, the grass may have provided some degree of concealment.

Nesting areas varied in the degree of refuge they provided for nests during inclement weather. Shorelines were often flooded during high winds or rainstorms. Islands, however, were rarely flooded and had the additional advantage that snow did not settle on them. Nesting areas farther from the water that were partially vegetated rarely were flooded, hence were good nesting sites during flooding; snow did settle in these areas during the blizzard, however. Hence, during bad weather birds that had nested on islands had an advantage.

In addition to being flexible in breeding activities, avocets are usually very effective in protecting their eggs from predators. Vigorous anti-predator behaviors may cause predators to concentrate on easier prey. Ducks, for example, are very abundant at Benton Lake, and their nests are more often the subject of predation.

The ability of avocets to nest in several habitats, to nest in groups of variable density, to renest, to build up

nests in flooded areas, and to initiate nests throughout a two and a half month period is clearly adaptive. Not only do these attributes allow avocets to compensate for predation by utilizing different anti-predator strategies or different habitats, but they allow survival of at least some nests in times of unexpected weather conditions.

Unfortunately, however, there is no way of knowing from my data the rate of chick survival on the breeding grounds or during migration. Clearly year-round studies of these birds are needed to elucidate all aspects of reproductive success and survival.

## CHAPTER 4

### SEX AND AGE DIFFERENCES IN FORAGING ACTIVITY

This chapter is devoted to determining if avocets partition available food resources by age and/or sex. This is accomplished by: 1) describing the methods for capturing prey, prey capture rates, and foraging depths of individual avocets; 2) determining if avocets at Benton Lake forage randomly among the depths available to them and 3) determining whether the various sex and age classes of avocets differ in their foraging activities.

### METHODS

Avocets were categorized into four groups: adult males, adult females, old chicks (3-6 weeks old), and young chicks (0-3 weeks old). Each category was distinctive and readily identifiable. Birds having a cinnamon colored head, neck and chest and with upper wing surfaces and flight feathers bearing three black bands were considered adults. Among adults, the sexes were separated on the basis of bill length and shape: males have a long slightly recurved bill, females a noticeably shorter, more recurved bill. Chicks were recognized by their smaller size and short straight bills. Chicks with a grey head and black fringing on their coverts forming an indistinct black stripe on the lower edge of

their wings were classified as young. Chicks with a pale pink head, and with two broad black bands on the wings and primary flight feathers were considered old.

Data were collected using binoculars, a spotting scope, and a tape recorder. Observations were spread throughout all daylight hours. All quantitative behavioral data were recorded using the focal-animal technique at fixed intervals of one minute (Altmann 1974).

Prey-capture methods of actively foraging avocets were recorded for a total of 437 min: males for 158 min, females 105 min, old chicks 81 min, and young chicks 57 min. The number of times each prey-capture method was used, and the number of captures of prey made per minute with each method, were recorded for one minute intervals. The sex and age class of the bird being observed, as well as the date and time, were recorded. Captures of prey were recorded as the number of swallows; it was impossible to determine the number of prey obtained with each swallow.

Depths of water at which avocets stood while foraging were recorded as the percentage of the birds' leg that was under water (% leg coverage or % LC). A total of 3931 observations were collected on foraging depths: 1427 observations were collected for males, 1101 for females, 596 for old chicks, and 447 for young chicks.

During June 1983, I measured depths of water available for foraging in unit VI south of island 12 (Fig 1-1) by

means of a series of transects. Water depth was measured with a meter stick. Depths of water at which avocets in this area stood while foraging during a two week period were translated into absolute depths by using known average leg lengths for male and female avocets.

## RESULTS

### Absolute Water Depths

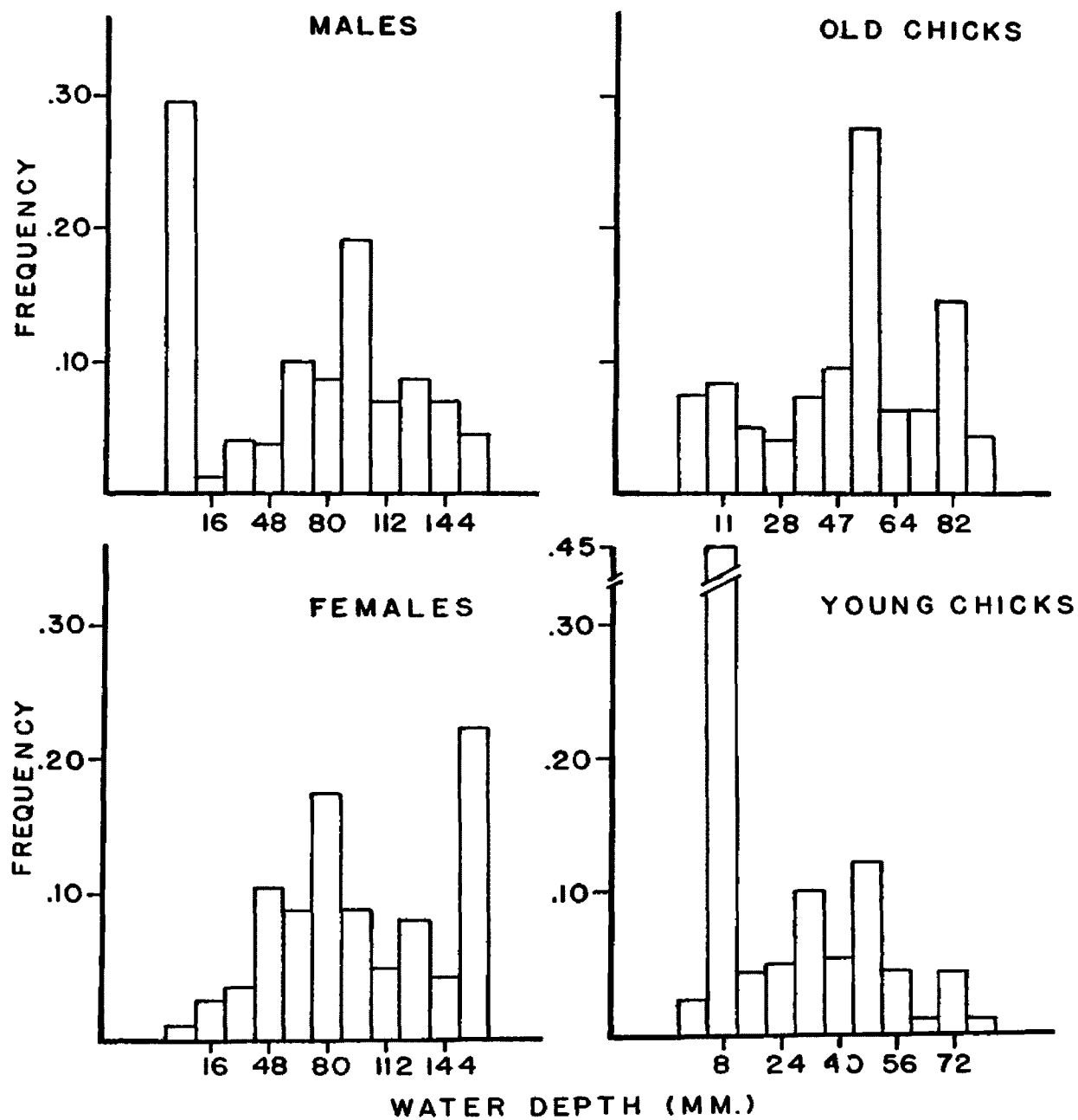
Adult avocets at Benton Lake rarely foraged on land, but chicks often did. Sometimes avocets foraged in flocks of up to 100 birds, at other times in smaller groups of 3-4 birds, and sometimes alone. Foraging adult avocets most often used the shallower sections of the lake, < 1 m, but the two sexes and each of the age classes of chicks used the water depths in different proportions (Fig 4-1). Young chicks used depths ranging from 0-90 mm but foraged almost half of the time (45%) at approximately 8 mm. Old chicks used depths of 0-100 mm but foraged most frequently (28%) at approximately 53 mm. Adults foraged at depths of 0->180 mm. Females had a bimodal distribution and foraged most often at approximately 81 and >155 mm, whereas males spent most of their foraging time at approximately 4 and 100 mm.

### Depths Relative To The Bird

Adult avocets did not use the available relative depths randomly (Fig 4-2). Instead they foraged at 50% LC and 100% LC far more frequently than would be expected if they fed

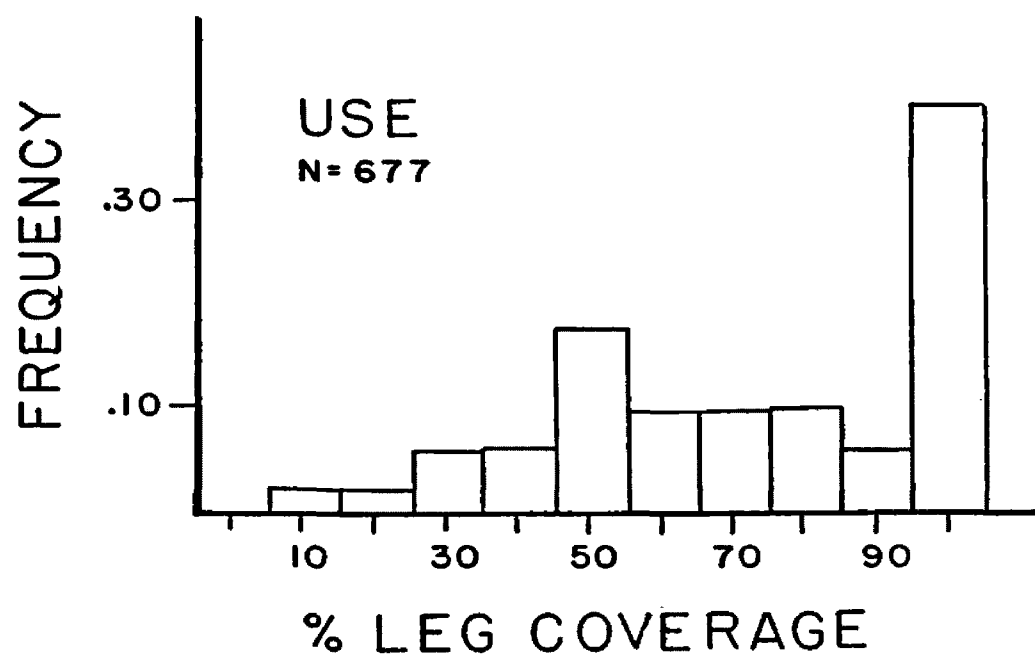
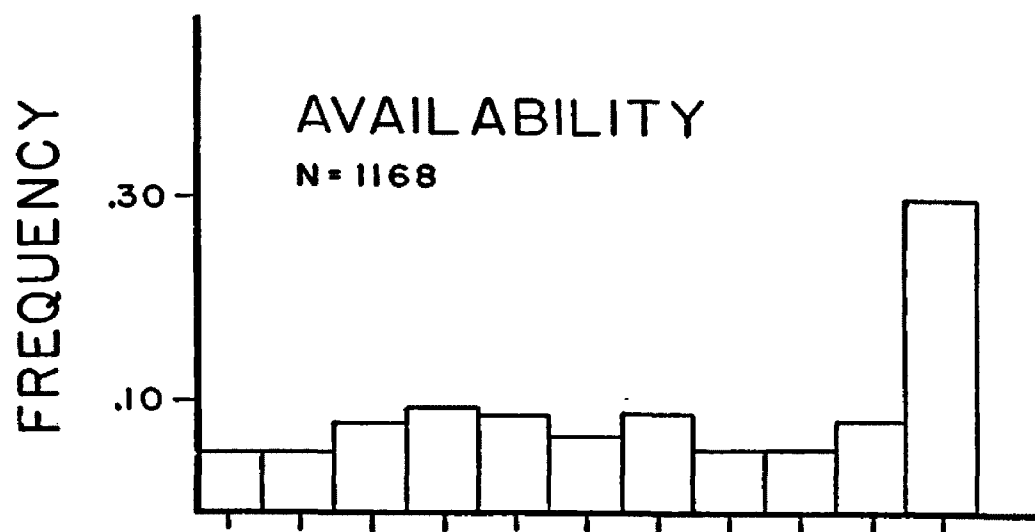


Fig 4-1. Frequency of foraging by adult males, adult females, old and young chicks at the various water depths. X-axes are different because of the different average leg lengths for each category of avocet.



46a

Fig 4-2. Frequency of occurrence and frequency of adult use  
of relative depths.



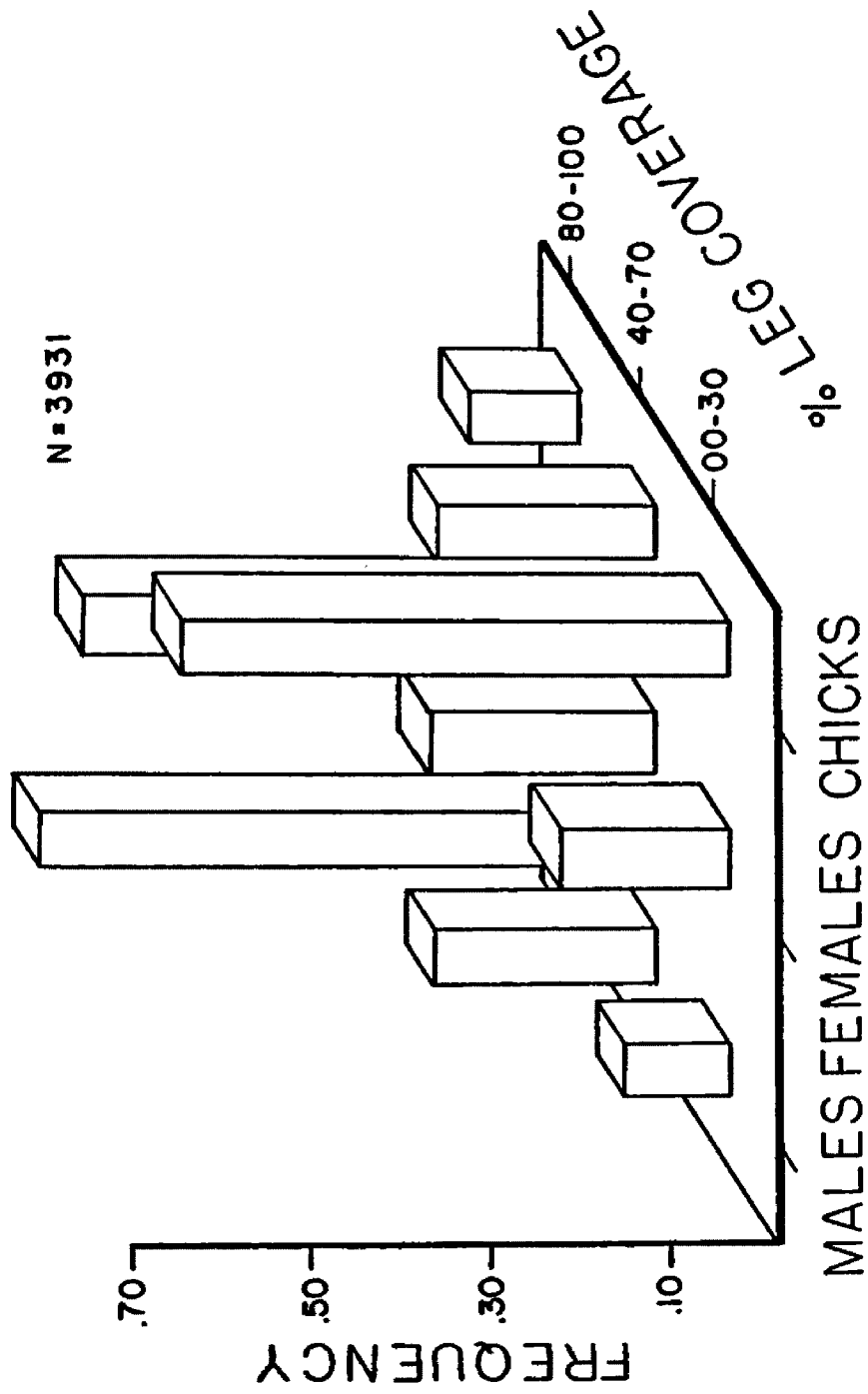
randomly with respect to depth (chi sq. = 169.0,  $p < 0.001$ ,  $df = 10$ ). Although both sexes spent most of their time (58%) foraging in 80-100% LC, males fed at 80-100% LC significantly more frequently than did females, while females fed at 00-30% LC significantly more often than did males (chi sq. = 19.8,  $p < 0.001$ ,  $df = 2$ ).

In contrast to adults, chicks foraged 61% of the time while in 00-30% LC; significantly different from the adults (chi sq. = 1009.0,  $p < 0.001$ ,  $df = 2$ ; Fig 4-3). However, the two classes of chicks differed in their use of water depth (Fig 4-4). Young chicks foraged at 00-30% LC significantly more commonly than did old chicks, who in turn fed at 40-70% LC significantly more often than did young chicks (chi sq. = 80.4,  $p < 0.001$ ,  $df = 2$ ). Young chicks, especially those less than seven days old, spent a substantial amount of time foraging on dirt or mud whereas old chicks foraged in such areas much less frequently, and adults only rarely.

#### Diurnal Patterns Of Foraging

Avocets fed at different depths at different times of the day (Table 4-1; Table 4-2). During the first ten hours of all days combined (0600-1600), chicks fed at 00-30% LC. During the last six hours (1600-2200) the majority foraged in 40-70% LC. Adults foraged at various depths during the first ten hours of all days combined, however during the last six hours most foraged in 80-100% LC.

Fig 4-3. Frequency of foraging at different relative depths  
for three groups of avocets.



49a

Fig 4-4. Frequency of foraging at different relative depths  
for old and young chicks.



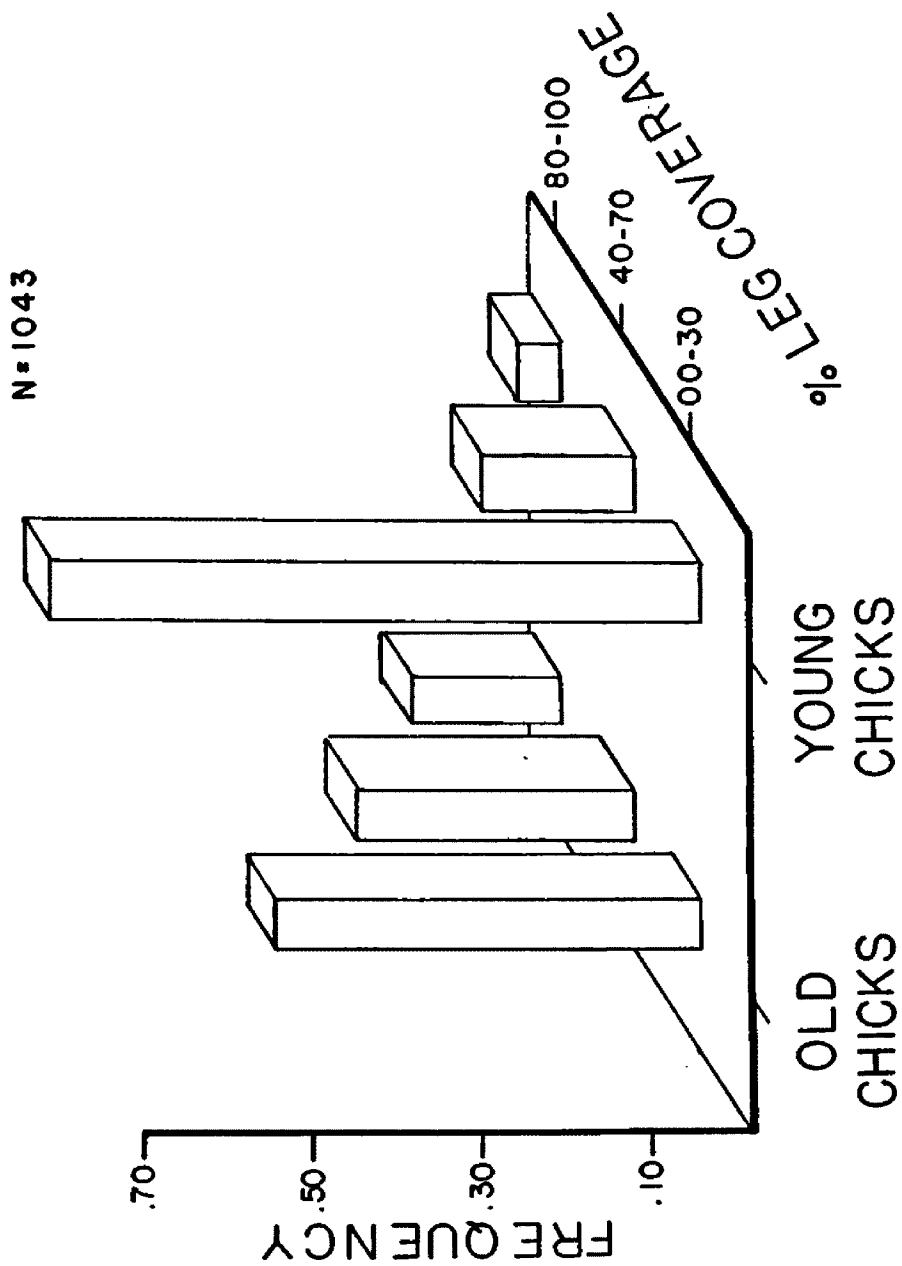


Table 4-1. Temporal use (%) of relative depths of water during foraging by all adult avocets.

Time of day	Relative water depth			Total No. of minutes
	00-30% LC	40-70% LC	80-100% LC	
0600-0800	15.1%	43.0%	41.8%	251
0800-1000	18.2%	35.2%	46.6%	423
1000-1200	18.4%	43.7%	37.9%	206
1200-1400	27.5%	67.5%	2.5%	40
1400-1600	48.6%	22.5%	25.0%	37
1600-1800	30.9%	32.3%	36.8%	136
1800-2000	9.8%	25.6%	64.7%	133
2000-2200	10.0%	37.1%	52.8%	70

Table. 4-2. Temporal use (%) of relative depths of water during foraging by all avocet chicks.

Time of day	Relative water depth			Total No. of minutes
	00-30% LC	40-70% LC	80-100% LC	
0600-0800	80.9%	8.7%	10.4%	241
0800-1000	52.6%	41.5%	5.8%	171
1000-1200	83.1%	8.8%	8.1%	260
1200-1400	58.8%	14.7%	26.5%	68
1400-1600	95.9%	4.1%	0.0%	169
1600-1800	18.5%	26.0%	11.0%	308
1800-2000	38.8%	40.9%	20.3%	276
2000-2200	44.8%	47.6%	7.5%	252

Chicks had a strong tendency to forage at lesser depths in the morning (0600-1000) and at mid-day (1000-1600) than during the evening (1600-2200) (chi sq. = 208.8,  $p < 0.001$ ,  $df = 4$ ). In adult females, the difference was less strong but statistically significant (chi sq. = 41.7,  $p < 0.001$ ,  $df = 4$ ). Adult males had the weakest tendency to move to deeper water (chi sq. = 20.7,  $p < 0.001$ ,  $df = 4$ ); however, since males foraged mainly in 80-100% LC, any move to deeper water would simply have been recorded as 100% LC, even though the absolute water depth might have been greater (Table 4-1; Table 4-2).

#### Adult Foraging Before And After Hatch

After the chicks hatched, adults remained close to them and chased intruders, both other avocets and individuals of other species away. Commonly adults took turns standing nearby, apparently "guarding", the chicks, one parent guarding while the other adult moved to deeper water to feed. Adults fed at distances ranging from 0 to 150 m away from their chicks. Family units including young chicks were easily distinguished because members remained close together. Family units with old chicks were less readily distinguished since the adults and chicks ranged farther from each other. Even though adults tended chicks in shallow water, the relative depths at which adult avocets foraged after chicks were hatched did not differ

significantly ( $\chi^2 = 0.4$ ,  $p > 0.50$ ,  $df = 2$ ) from those at which they fed before the chicks hatched (Table 4-3).

#### Prey-Capture Methods

Avocets used five prey-capture methods: Peck, Plunge, Land/Top Peck, Bill Pursuit, and Scythe.

**Peck (PE).** Pecking involved the grabbing of an item from the water with a jab of the bill. The bill was immersed in the water but the head was never submerged. Prey were taken from the top few cm of water.

**Land and Top Peck (LT).** A motion similar to pecking was used to take prey from on land or off the surface of mud or water. The bill was not immersed in the water.

**Plunge (PL).** Plunging involved a grabbing motion similar to pecking but the head, and sometimes the neck and breast, entered the water. Thus, prey were taken from a deeper layer of water than in pecking. Usually the bill and head were withdrawn smoothly from the water after the plunge, but occasionally the bill was rapidly and erratically moved under the water before being withdrawn.

**Bill Pursuit (BP).** In bill pursuit, the bill was rapidly opened and closed while simultaneously moving erratically along the water's surface. This method of capture was used mainly to obtain rapidly moving invertebrates on the surface of the water.

**Scythe (SC).** In this method of feeding the side of the slightly opened bill was placed flat on the water's surface

Table 4-3. Adult use of relative depths before and after their chicks hatch.

	Relative depth						Total no. of min.
	00-30% LC		40-70% LC		80-100% LC		
	No. of min.	%	No. of min.	%	No. of min.	%	
before hatch	153	25.3	212	35.0	240	39.7	605
after hatch	34	27.9	42	34.4	46	37.7	122

to one side of the avocet's midline and then moved rapidly to the opposite side of the body. Usually the bird raised its head to swallow after a single such motion but sometimes the bill was moved rapidly from side to side several times before the head was lifted.

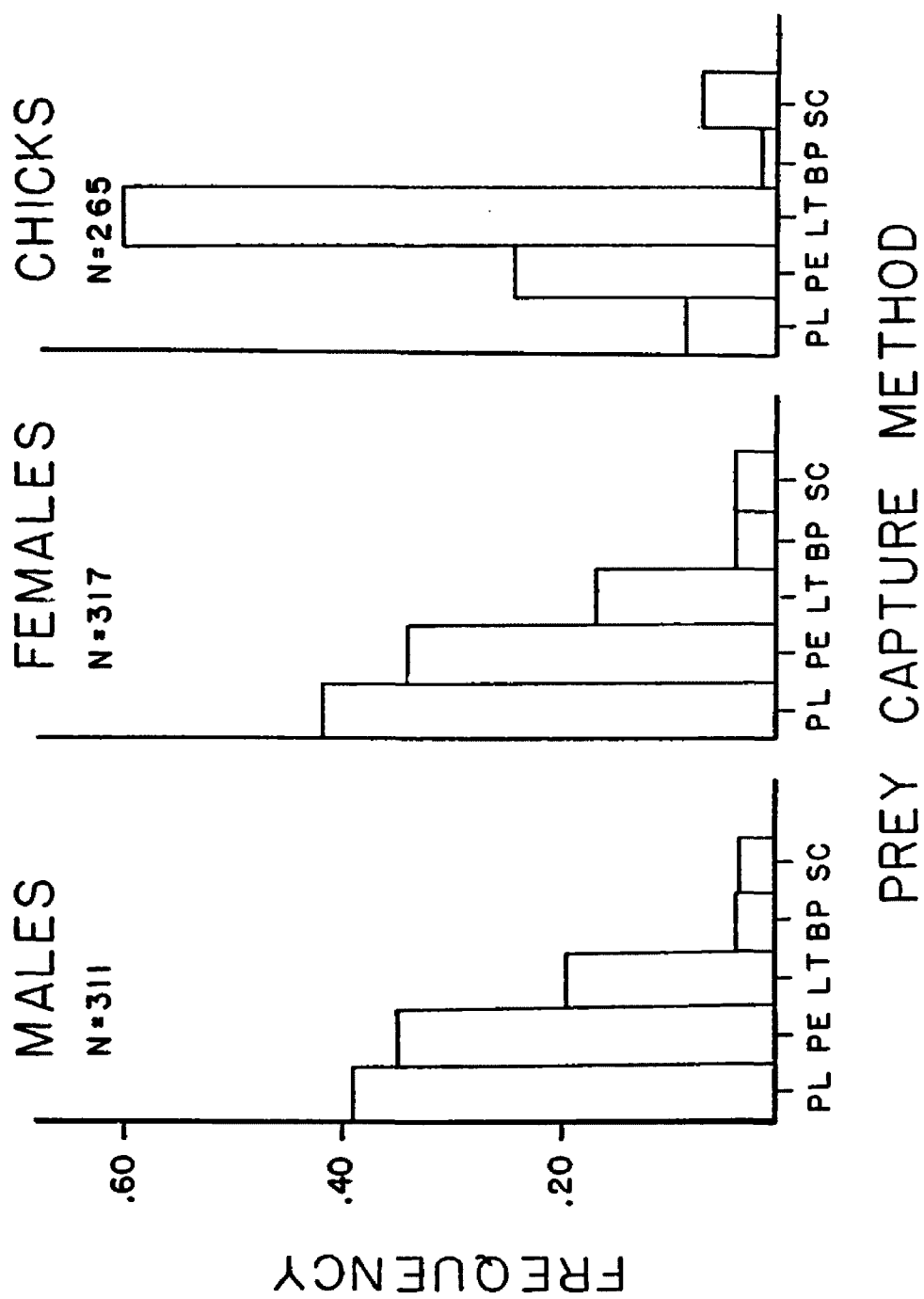
#### Variations In Use Of Prey-Capture Methods

Avocets did not use methods of prey-capture randomly (chi sq. = 365.8,  $p < 0.001$ ,  $df = 4$ ; Fig 4-5). All adults combined used PE and PL more than would be expected (chi sq. = 316.0,  $p < 0.001$ ,  $df = 4$ ), and all chicks combined used LT more than expected (chi sq. = 299.9,  $p < 0.001$ ,  $df = 4$ ), if the prey-capture methods were used randomly. Although adult males and females did not differ significantly from each other in the frequency with which they used each foraging method (chi sq. = 0.9,  $p > 0.50$ ,  $df = 4$ ), females and males combined did differ significantly from chicks (chi sq. = 56.8,  $p < 0.001$ ,  $df = 4$ ). The two classes of chicks foraged principally (60%) off the surface of the water or on land. Classes of chicks differed significantly (chi sq. = 9.1,  $p < 0.05$ ,  $df = 4$ ); young chicks used LT more often (70%) than old chicks (61%; Fig 4-6). On the other hand, old chicks used PL (11%) more often than young chicks (1%).

Avocets did not use different prey-capture methods at different times of the day (chi sq. = 8.99,  $0.05 < p < 0.10$ ,  $df = 4$ ). Although all categories of avocets tended to forage

Fig 4-5. Frequency of foraging with different prey capture methods for three groups of avocets. PL=plunge, PE=peck, LT=land/top, BP=bill pursuit, SC=scythe.



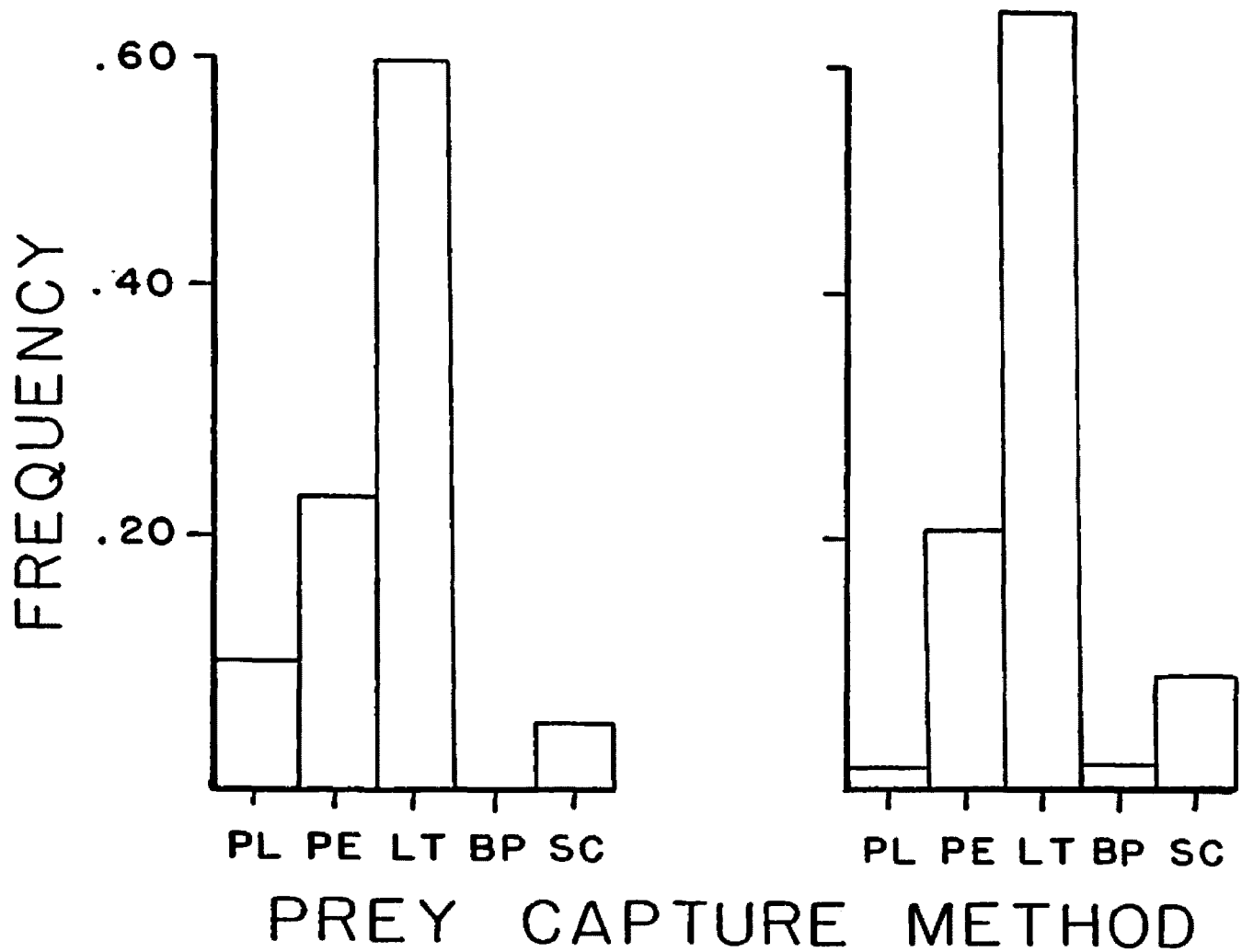


57a

Fig 4-6. Frequency of foraging with different prey capture methods for old and young chicks. PL=plunge, PE=peck, LT=land/top, BP=bill pursuit, SC=scythe.

OLD  
CHICKS  
N=128

YOUNG  
CHICKS  
N=79



in deeper water in the evening, they tended to use the same prey-capture methods they used in shallower water.

#### Temporal Patterns Of Foraging Activity

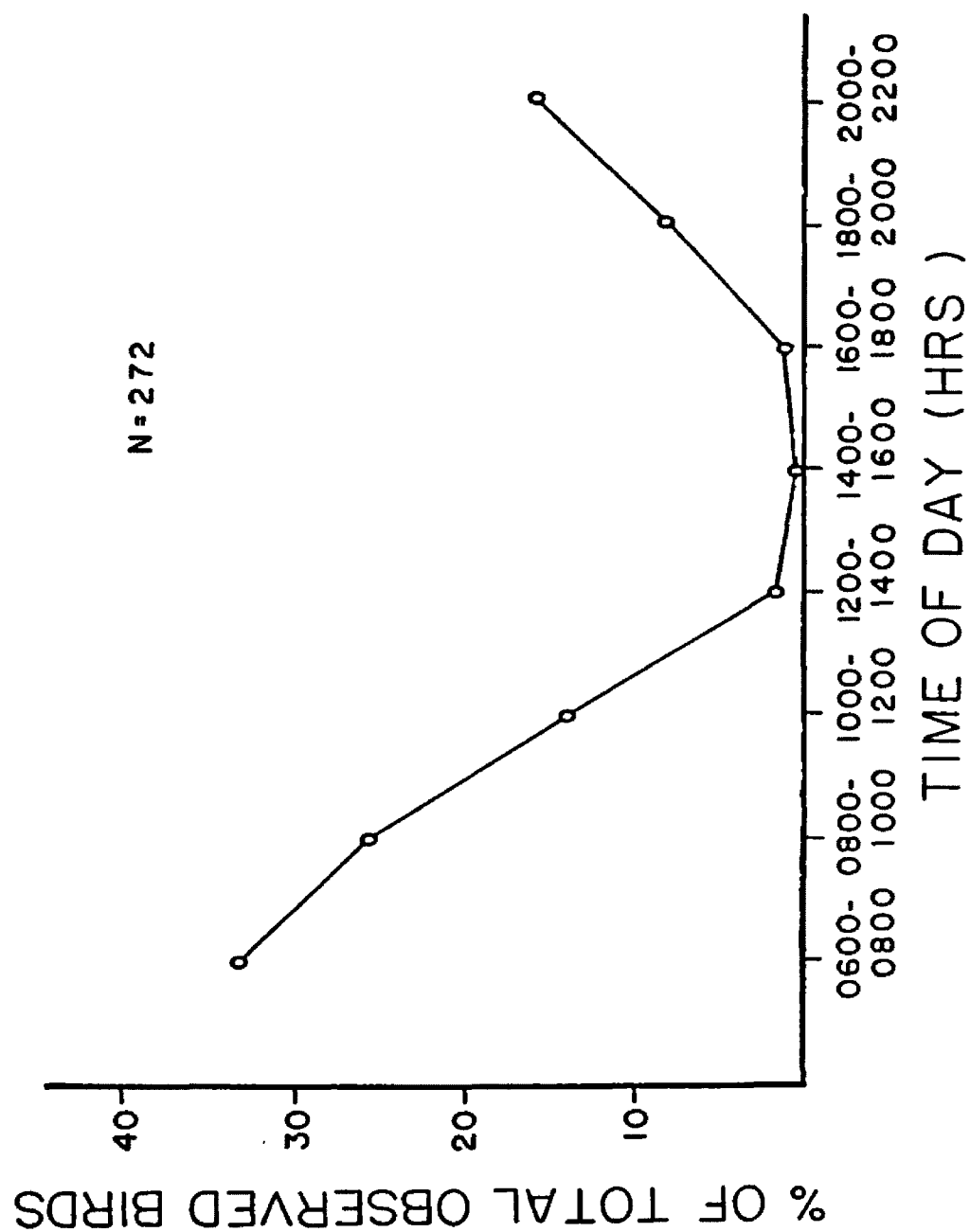
Avocets had a bimodal feeding pattern with a peak of activity from sunup to approximately 1030 and a secondary peak from about 1930 to sundown (Fig 4-7). From 13 to 16 June 59.4% of all birds observed foraging in unit VI, south of island 12 were seen between 0600-1000. Birds foraging in the six midday hours (1000-1600) accounted only for 16.2%. Another 24.3% of the observed foraging birds were seen in the six evening hours (1600-2200). Although no testable data were collected, chicks seemed to feed during the middle of the day (1200-1600) much more often than did adults.

#### Variation In Prey Intake Rate

Rate of prey-capture varied depending upon water depth (Fig 4-8). Adults on the average captured prey most rapidly at 80-100% LC (27 swallows per min); prey-capture rates at intermediate depths of 40-70% LC (22 swallows per min) and 00-30% LC (23 swallows per minute) were significantly lower as tested with Mann-Whitney U (00-30% by 80-100%:  $U = 3024.5$ ,  $p < 0.04$ ; 40-70 by 80-100:  $U = 5214.5$ ,  $p < 0.001$ ). In contrast, all chicks combined captured prey most rapidly at 00-30% LC and 40-70% LC (27 swallows per min in each case); prey-capture rates at 80-100% LC were lower (20 swallows per min), but not significantly so (00-30% by 80-100%:  $U = 1261.0$ ,  $p < 0.14$ ; 40-70% by 80-100%:  $U = 638.0$ ,  $p < 0.15$ ). Old

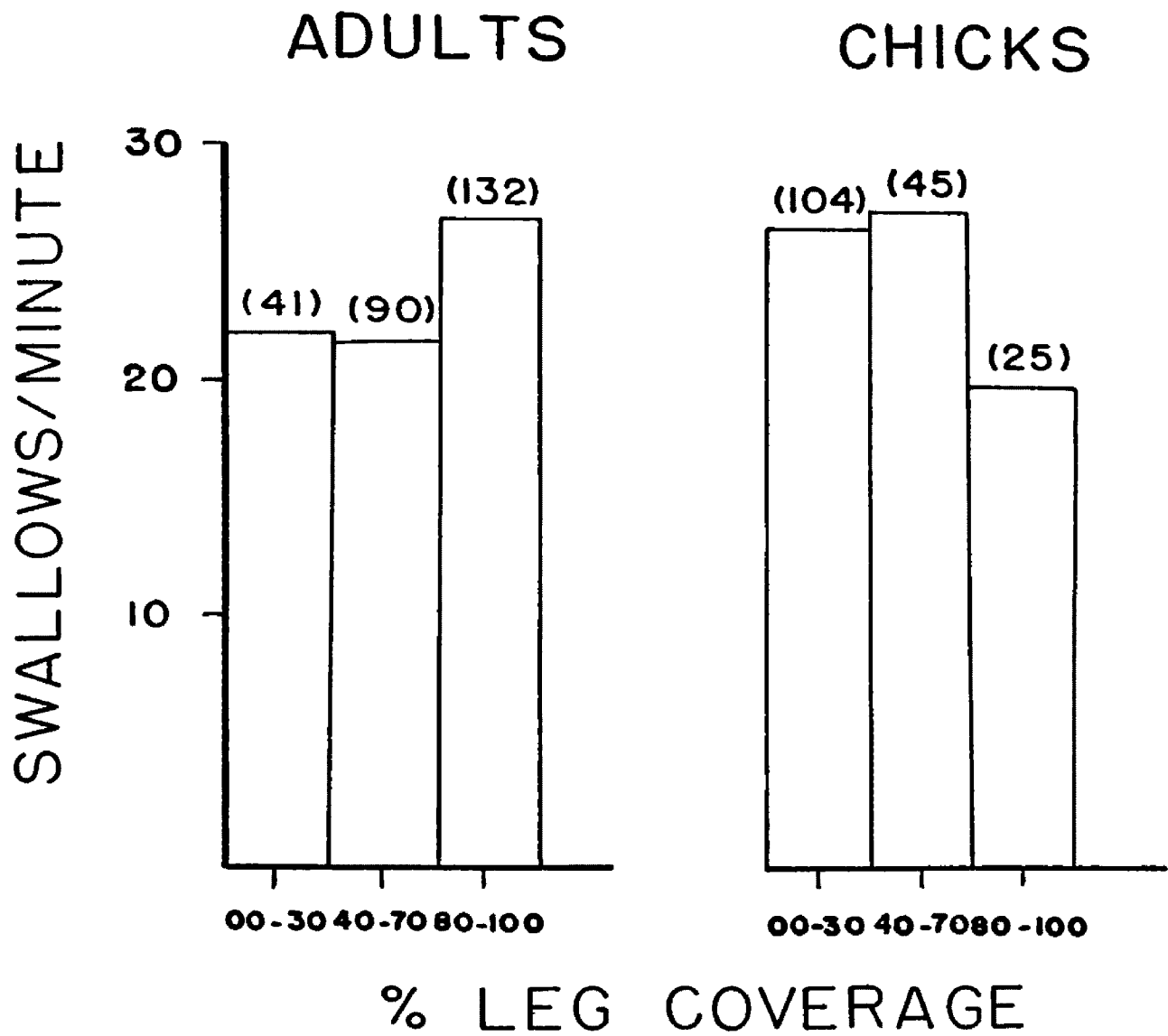
59a

Fig 4-7. Percent of total observed avocets foraging in each two-hour time block throughout daylight hours.



60a

Fig 4-8. Capture rates (swallows per minute) of adults and chicks while foraging at different relative depths. Numbers in parentheses indicate number of minutes.





chicks were most effective at 40-70% LC (37 swallows per min); capture rates were less at 00-30% LC (31 swallows per min) and considerably less at 80-100% LC (19 swallows per min). These differences are statistically significant as tested with Mann-Whitney U (00-30% by 40-70%:  $U = 514.0$ ,  $p < 0.01$ ; 00-30% by 80-100%:  $U = 330.5$ ,  $p < 0.04$ ; 40-70% by 80-100%:  $U = 236.5$ ,  $p < 0.001$ ). Young chicks were more effective at capturing prey at 00-30% LC (24 swallows per min) than at 40-70% LC (23 swallows per min) but not significantly so (00-30% by 40-70%:  $U = 234.0$ ,  $p < 0.16$ ); young chicks did not forage at 80-100% LC (Fig 4-9). A comparison between young and old chicks reveals that old chicks had a higher rate of prey intake than did young chicks at all depths; the difference in prey-capture rates were statistically significant (chi sq. = 22.4,  $p < 0.001$ ,  $df = 4$ ). Old chicks had a higher prey intake rate than adults at 00-30% LC and 40-70% LC, but adults were much more effective at 80-100% LC.

Methods of foraging were not equally effective for all age and sex categories (Fig 4-10). Adults were most successful in capturing prey using PL (21 swallows per min) and PE (10 swallows per min). While the difference was not statistically significant, females were slightly more effective in gathering prey with PE and males with PL (PE: chi sq. = 8.7,  $0.20 < p < 0.10$ ,  $df = 5$ ; PL: chi sq. = 15.3,  $0.10 < p < 0.05$ ,  $df = 8$ ). Chicks (all ages combined) were most

Fig 4-9. Capture rates (swallows per minute) of old and young chicks while foraging at different relative depths. Numbers in parentheses indicate number of minutes.

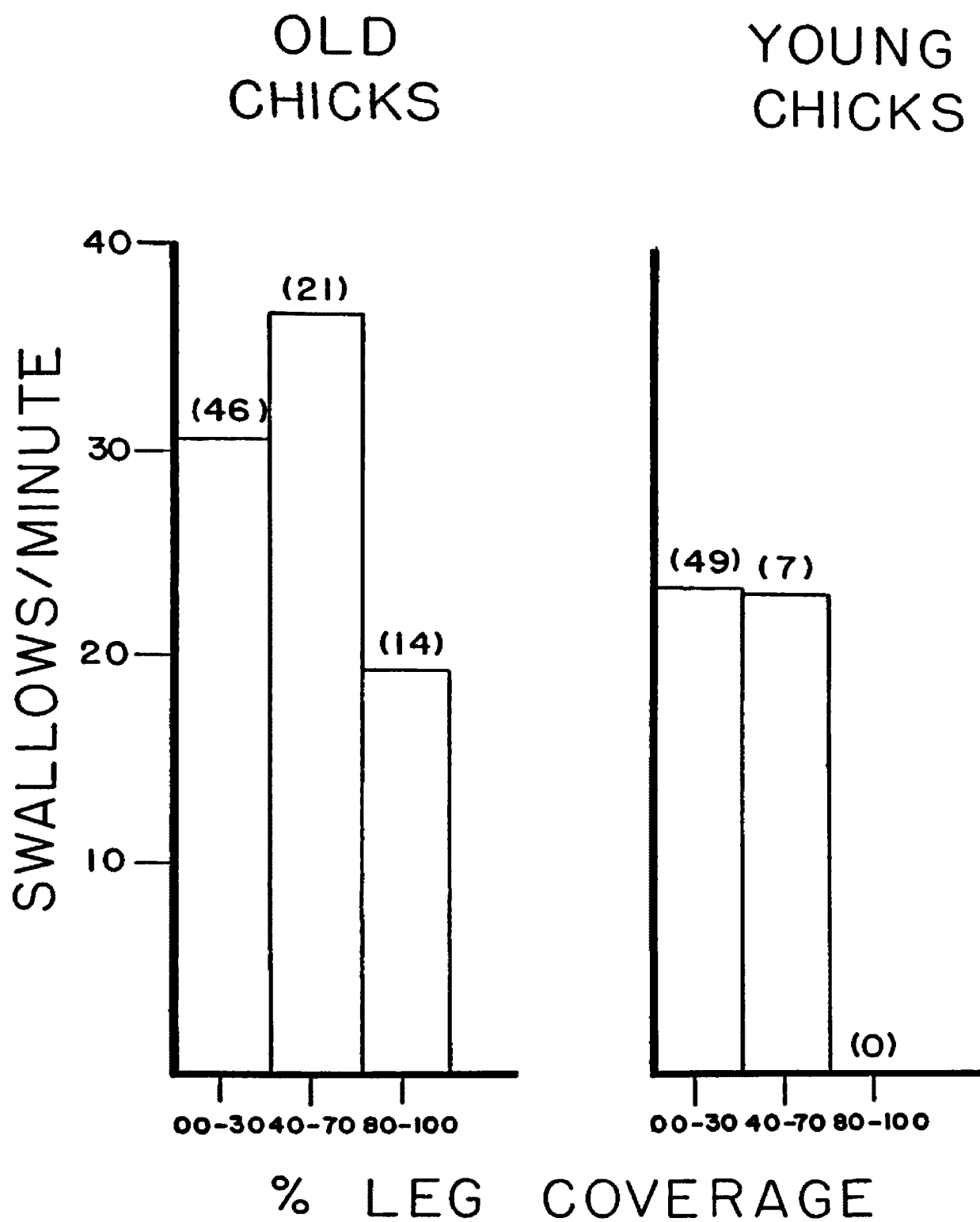
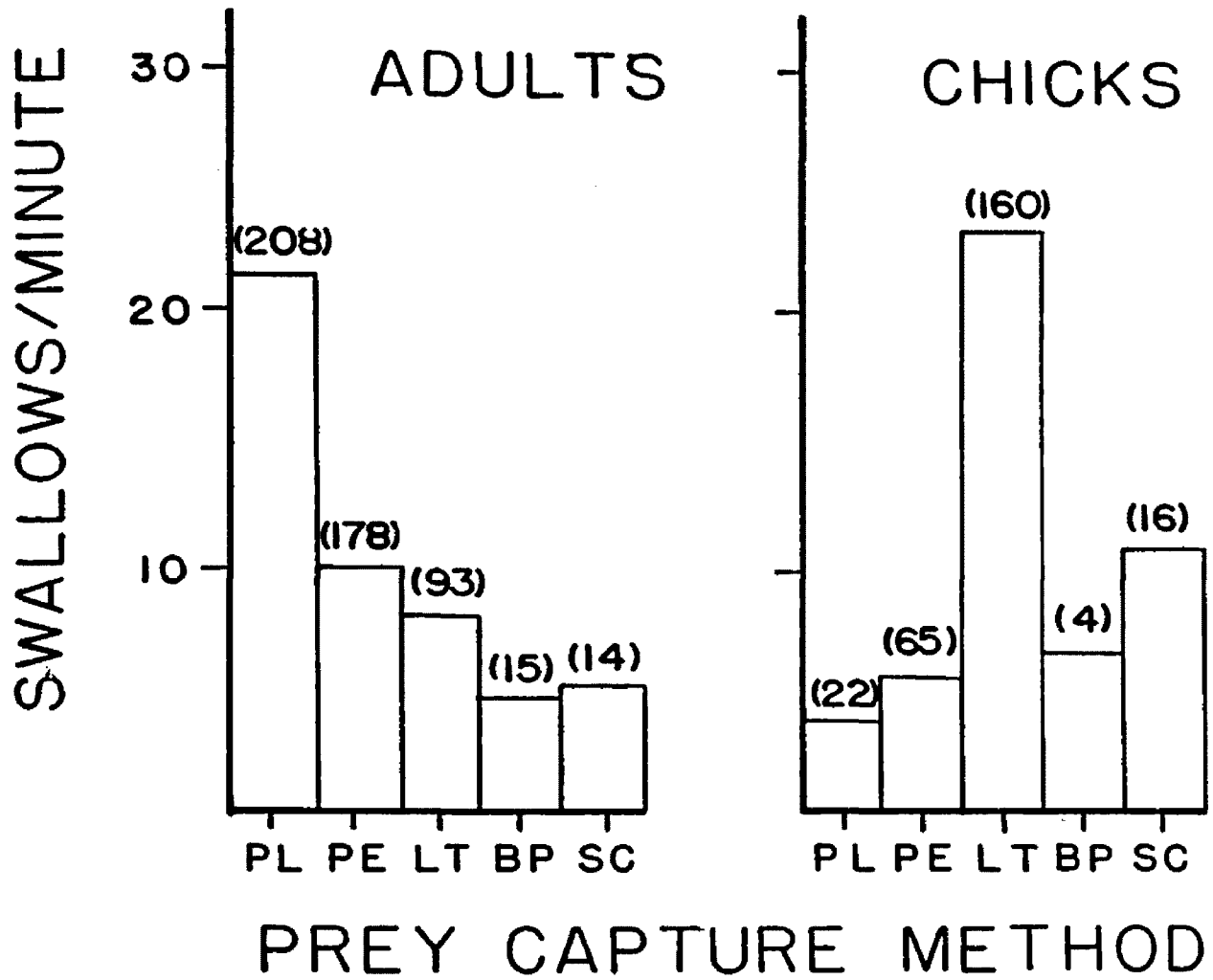


Fig 4-10. Capture rate (swallows per minute) of adults and chicks while using different prey capture methods. PL=plunge, PE=peck, LT=land/top, BP=bill pursuit, SC=scythe. Numbers in parentheses indicate number of minutes.



successful using LT (24 swallows per min). Adults were significantly better at PE and PL than were chicks (PE: chi sq. = 8.2,  $p = 0.05$ ,  $df = 4$ ; PL: chi sq. = 57.9,  $p < 0.001$ ,  $df = 3$ ) whereas chicks were significantly better at LT than were adults (chi sq. = 113.9,  $p < 0.001$ ,  $df = 8$ ). Old chicks had a higher prey-capture rate with every method than did young chicks (Fig 4-11).

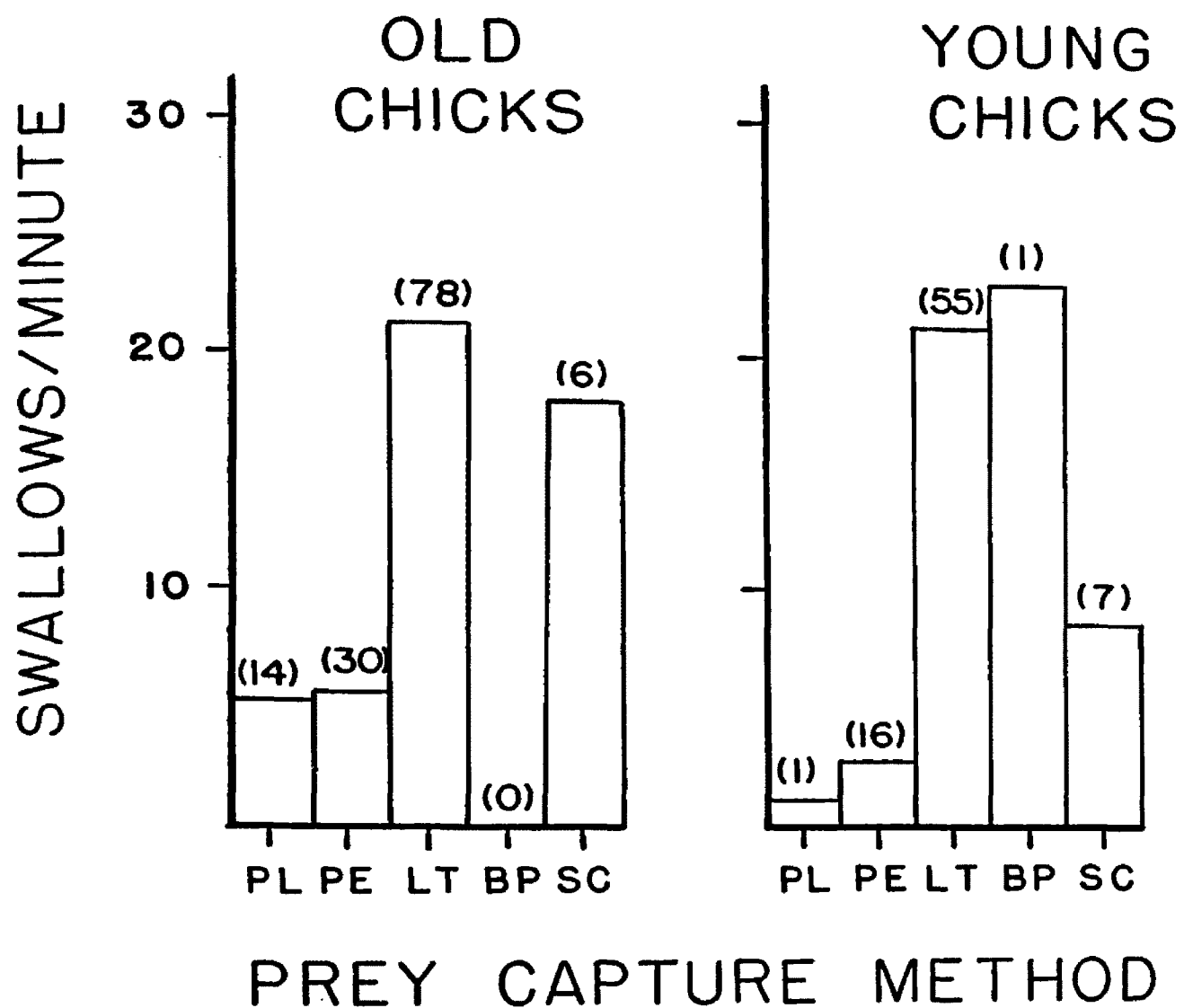
Average rate of prey-capture for all birds combined in all two-hour blocks (except 1200-1400) was approximately 25 swallows per min. From 1200-1400 foraging birds had an average prey-capture rate of only 14 per min, different from that during any other two-hour block. Average rate of prey-capture and number of birds feeding in each two-hour block were not significantly correlated as tested with the Spearman Rank correlation coefficient ( $r_s = 0.31$ ,  $p > 0.05$ ,  $df = 8$ )

## DISCUSSION

### Spatial Use Of Foraging Areas

Avocets at Benton Lake were nonrandom in the spatial use of their foraging areas. Young birds foraged mainly in very shallow water or on land, old chicks foraged in water of intermediate depths and adults foraged in the deepest water. Furthermore, young chicks tended to forage at 00-30% LC whereas old chicks forage predominantly at 40-80% LC. Adults generally forage at 80-100% LC, but the slightly

Fig 4-11. Capture rates (swallows per minute) of old and young chicks while using different prey capture methods. PL=plunge, PE=peck, LT=land/top, BP=bill pursuit, SC=scythe. Numbers in parentheses indicate number of minutes.





larger males did so even more than females. Thus, birds in each age/sex group foraged at relative depths that correlate generally with leg and bill lengths, leading to a horizontal separation of the feeding area within the species.

The tendency of chicks to forage on land and in shallow water probably results from several different factors. 1) Lacking practice or maturity the chicks may be unable to accurately direct their bills to the target, hence less able to capture prey in deeper water. 2) Chicks may be unable to adequately maneuver in deeper water. 3) Perceptual capabilities of the chicks may not be developed enough to allow them to perceive prey adequately in deep water. 4) Chick preference for shallow water may be related more to predator avoidance, the depths at which they feed merely a function of the distance to nearest cover. 5) Failure to use deep water may be related to leg length, bill length and/or bill shape.

Evidence indicates that increasing practice does influence coordination and ability to capture prey. For instance, young chicks captured fewer prey per minute with all methods and at all depths of water than did old chicks. Young chicks also are unable to swim proficiently, hence are less likely to capture prey in deep water. A similar change in foraging behaviors attributed to experience has been reported for juvenile Reed Warblers (Acrocephalus scirpaceus; Buckley and Buckley 1974; Davies and Green 1976;

Davies 1976a). Foraging efficiency has also been reported to increase with age and practice in mammals such as lions (Bertram 1975) and mountain gorillas (Schaller 1967, 1972).

Evidence collected from avocets does not indicate whether changes in perception occur as the chicks grow but Reed Warblers have been reported to undergo perceptual changes as they mature (Davies and Green 1976; Davies 1976a). Perceptual changes are also thought to occur in insectivorous forest birds as they learn to identify cryptically colored prey (Fogden 1972).

Young chicks may prefer to forage near the edge of the water simply because cover is within easy reach. This is supported by the fact that chicks often foraged in shallow areas where cover was abundant, but only rarely in equally shallow areas away from cover. They also avoided deeper areas near cover suggesting that both cover and water depth are critical.

The use of foraging depths by avocets probably is related to bill shape and size because preferred foraging depths clearly vary with length of bill. Birds with the longest bills forage in the deepest water. Chicks with their short straight bills, are able to capture prey near the surface of water and in shallow water but are less effective foragers in deeper water where prey swim deeply and perhaps sit on the bottom. Adults, especially males, are effective foragers in deeper water because of their much

longer bills; on the other hand, for them, prey at the edge of the water may not be so easily obtained with the recurved bill. Thus, each bill morphology may allow an avocet to forage most effectively at certain depths.

Male and female American Avocets at Summer Lake, Oregon generally feed in different areas (Gibson 1978). Adults may subdivide resources between the sexes by a divergence of bill shape (Hamilton 1975). Other bird species also have different feeding niches dependent upon bill shape and size. Galapagos finches (Geospiza fortis and G. scandens) show intra-population variation of foraging areas that correspond with size of bill (Grant et. al. 1976). The longer bill and tarsus and the shorter wings of Long-billed Dowitchers (Limnodromus scolopaceus) are thought to permit foraging in water of greater average depth than Short-billed Dowitchers (Limnodromus griseus), a very similar species (Pitelka 1950). The great structural disparity between the sexes of these species may also increase total foraging area. Other birds, for example, male and female Henslow's Sparrows (Ammodramus henslowii) are known to partition their feeding areas even though there are no distinguishable differences between the sexes (Robins 1971). A similar method of partitioning has been demonstrated for Winter Wrens, Troglodytes troglydytes (Harrison and Buchan 1934; Armstrong 1955) and for warblers in a spruce forest (Morse 1968b), all sexually monomorphic species.

### Temporal Patterns In Foraging

The bimodal temporal foraging patterns among avocets may be due to heat stress during the middle of the day (Ricklefs and Hainsworth 1968; Spurr and Freedden 1978), to changes in food availability (Hutto 1981), to changes in prey detectability (Hailman 1984) or to a motivational change in the bird (Morton 1967; Kessell 1976). Avocets at Summer Lake, Oregon, demonstrated a similar bimodal feeding pattern but only during the prenesting and post-breeding periods. During incubation and parental-care periods the bimodal pattern was not obvious, possibly due to need to spend much time with eggs and young (Gibson 1978). Diurnal patterns of foraging at Benton Lake also appeared to be somewhat modified during parental care, but the bimodal pattern was still evident. Similar bimodal patterns of foraging have been described for many other avian species, particularly insectivorous birds (Ricklefs and Hainsworth 1968; Ricklefs 1971; Austin and Smith 1972; Diamond 1973; Dyer 1974; Ratkowsky and Ratkowsky 1978; Greenwood and Harvey 1978; Craig 1978; Hutto 1981).

Adult avocets tended to forage in deeper water in the evening than in the morning or at midday. This shift may be because prey density in shallow water becomes depleted later in the day, but this is unlikely. More likely the birds are following horizontal or vertical migrations of their invertebrate prey.

### Prey-Capture Methods And Prey Intake Rates

The tendency of avocets of varying ages and sexes to use the various methods of prey-capture in different proportions, could be a result of any of several factors. Among the most obvious are: 1) differences as a result of experience; 2) variation in position in dominance hierarchies; 3) morphological characteristics such as bill size and shape, body size, leg length or tail length; 4) difference in prey distribution and abundance in different habitats.

Experience and learning do not seem to greatly affect the methods of prey-capture that avocets use. This is suggested by the fact the chicks use the entire repertoire of prey-capture methods; only the proportion of use changes. It is possible, however, that they may become more effective at using some techniques through experience. Learning is known to affect foraging patterns in other avian species. Among hand reared Great Tits (Parus major) variations in foraging patterns were attributed to differences in experience (Partridge 1976). Oystercatchers (Haematopus sp.) have been reported to learn feeding techniques directly from their parents and may learn either to stab or to hammer, but not both (Norton-Griffiths 1967, 1969).

No evidence is available to indicate whether foraging patterns among avocets are related to a dominance hierarchy,

since individual avocets were not identified and no dominance hierarchy observed. Foraging in some woodpeckers however, is related to position in dominance hierarchies (Ligon 1968a; Hogstad 1978a).

The relationship between morphological characteristics, particularly of the bill, and foraging patterns is clear. Preferred feeding methods obviously vary with bill length, body size and leg length. Probably the most effective foraging technique varies with these morphological characteristics. Morphological characteristics also affect patterns of foraging in several other avian species. For instance, differences in foraging techniques in Boat-tailed Grackles (Quiscalus major) were attributed to difference in the size of tail (Selander 1966). Many sexual differences and corresponding foraging differences have been recorded for Carrion Crows, Corvus corone (Holyoak 1969); European Goldfinches, Carduelis carduelis (Newton 1967); Huis, Neomorpha acutirostris (Buller 1888); Red Eyed Vireos, Vireo olivaceus (Williamson 1971); Boat-tailed Grackles, (Selander 1966) and Hairy Woodpeckers, Dendrocopus villosus (Kilhan 1965). Galapagos finches (Geospiza fortis and G. scandens) showed variations in food selected that corresponded to bill size (Grant et. al. 1976).

Each of the various methods of prey-capture used by avocets is probably most effective in specific habitats. Foraging techniques must affect both type of prey and amount

of prey caught and, consequently, the rate of energy intake. Avocets spend much of their life foraging on coastal areas. During the winter, avocets foraging in the coastal areas on Humboldt Bay, California, scythe more often than they use any other foraging method (Evans pers. comm.) In contrast, avocets at Benton Lake scythed rarely and most often were observed scything in very shallow water or during very strong winds accompanied by rain, conditions that may have created an invertebrate distribution similar to that on the coast. Though indirect, this evidence may indicate that distribution and availability of the prey does influence method of prey-capture in avocets. Similar seasonal changes in patterns of foraging behavior have been recorded in six other species of shorebirds (Baker and Baker 1973). Five of the six species became behaviorally more diverse during the summer.

Adults generally had higher capture rates than chicks with all methods and at all depths. Old chicks were better than young chicks at capturing prey at all depths and with all methods. However, the difference in prey-capture rates between avocet adults and chicks is not large. This may be because small aquatic invertebrates are fairly easy prey with which to cope, even for inexperienced chicks. In contrast, mammalian species that feed on large prey such as lions may take years to become proficient at capturing prey (Schaller 1967, 1972; Bertram 1975). In general, the

greater the difficulty in coping with a prey item, the greater the difference one would expect to find in prey intake rate between age classes (Morse 1980). Because avocet prey are small relative to the bird at all ages, differences in rates of prey-capture between age classes may be less than in many other birds or animals.

### Conclusion

Different categories of avocets show differences in spatial use of the foraging area, methods of prey-capture used and rate of prey-capture. These differences may result in partitioning of foraging areas by method and depth. Temporal partitioning was not measured directly but appears to be occurring because the chicks tend to forage more often during the middle of the day than the adults. Actual partitioning of food resources has not been addressed because of the difficulties in effectively sampling abundance and distribution of aquatic invertebrates at the various depths.

The change in bill morphology as the chicks grow may cause the characteristics of the foraging niche of this species to be dynamic and fluid. The chicks' bill morphology may allow them to forage in areas where prey are abundant and competitors few. Few other species of birds at Benton Lake use the prey source at the edge of the water. Only Willet chicks (Catoptrophorus semipalmatus) were occasionally seen foraging at the edge of the water at the



time avocets were using it. Although Long- and Short-Billed Dowitchers forage in this area, they continue their migration long before avocet chicks hatch. Adult avocets avoid competition with their chicks by foraging in deeper water and, consequently, their offsprings' chances of survival are improved.

Partitioning is usually assumed to occur when there is a limiting resource such as food. However, many indirect data indicate that food at Benton Lake is not limiting to avocets. A variety of invertebrates were seen emerging every week and there were often large masses of them in windrows along shorelines during the breeding seasons of both years of the study. Furthermore, avocets spent much of their time resting and performing activities other than feeding, suggesting they were able to obtain sufficient food in brief periods of foraging. The fact that the birds were able to recover from a severe blizzard that destroyed their initial clutches, lay a second clutch, and hatch 70-80% of these eggs suggests the availability of an ample supply of food since this hatching rate is comparable to those reported of avocets with first clutches elsewhere in the United States. Several studies on other bird species also have shown that there is usually no shortage of food on the breeding areas (Kilhan 1965; Goss-Custard 1970; Green and Hobson 1970; Hughes 1970).

It is possible however, that the food partitioning is much more critical in the wintering grounds where food may be more limited. Although no data specifically regarding avocets are available, several investigators have reported that other species of shorebirds that do not show intra-population differences in feeding areas, in behavior patterns, or in prey taken on breeding grounds, do show such differences in wintering areas (Ehlert 1964; Recher 1966; Holmes 1966a). A combination of less total daylight, higher tides, and perhaps abundance, density and distribution of prey may be responsible for the greater impact of winter food conditions on the birds (Lenna and Ralph 1967; Goss-Custard 1969; Heppleston 1971). If food were limiting on the wintering grounds the distinct bill morphologies and different leg lengths of the avocets could reduce intra-specific competition.

It is also possible that the variation in bill structure among avocets may be related to factors other than feeding, such as sexual recognition. The differences may have nothing to do with competition and may be due to growth and morphological constraints. But, regardless of their evolutionary origins, the structural dimorphisms provide a method by which the foraging areas and prey of the avocets may be partitioned. Year-round studies would help us understand the mechanisms by which the American Avocet reduces intra-specific competition.

## CHAPTER 5

### SUMMARY

American Avocets were studied during the 1983 and 1984 breeding seasons at Benton Lake National Wildlife Refuge in north central Montana where hundreds feed and nest. Breeding and foraging activities were documented, individual differences in breeding activities and factors influencing hatching success were recorded.

The questions I attempted to answer in this study were: 1) what is the hatching success, 2) what factors influence hatching success, and 3) does food resource partitioning exist among different age and sex classes of American Avocets at Benton Lake.

Avocet breeding activities extended over a four month period from mid-April to mid-August. Laying dates ranged from late April to early July; egg size, egg color and clutch size varied as well. Nests were placed in a variety of habitats such as islands, shorelines, and dry lake beds. Vegetation around nests ranged from tall mature grasses to short emergent grass to bare ground. Nests were scattered to varying degrees; some were placed within 5 m of the nearest other nest, others were placed farther away and some were solitary, more than 35 m from their nearest neighbor.

A blizzard in mid-May, 1983 disrupted the beginning of laying and delayed breeding for several weeks. Many avocets whose nests were destroyed produced replacement clutches, but clutch sizes were more variable than before the blizzard or in 1984 and fewer eggs hatched than in the following year. The blizzard also affected the placement of nests; birds nesting after the blizzard in 1983 generally nested closer to their neighbors than in 1984.

Hatching success during both years was high: 71% for 1983 and 79% for 1984. The most important factor influencing avocet hatching success seemed to be the nature of the nesting habitat. In 1983, nest-success of birds nesting on islands was significantly lower than that of birds nesting on shorelines; in 1984 nest success in the dry lake bed was higher than on shorelines. Hatching success also varied with clutch size. Birds that laid three and four eggs produced at least one hatchling far more often than those with one, two or more than four eggs. Laying date also influenced hatching success. Avocets that nested early in the season frequently lost their clutches as a result of low temperatures, snow, or flooding, whereas those nesting late in the season were commonly subject to predation. Avocets nesting between these two extremes hatched more eggs. Inter-nest distance and density of nests

also influenced hatching rate. Avocets nesting in areas with large inter-nest distances hatched more eggs than those who placed their nests closer to neighbors.

Ability of the avocets to nest in several habitats and in groups of variable density, to renest, to build up nests, and to initiate nests throughout a two and a half month period is clearly adaptive. Not only does it allow the birds to compensate for predation by utilizing different anti-predator strategies in different areas, but it allows survival of at least some nests in times of unexpected weather conditions. This extreme adaptability may contribute to their high hatching success.

Foraging behavior of four age/sex categories of avocets (chicks 0-3 weeks old, chicks 3-6 weeks old, adult females, adult males) was observed. Birds in each category foraged at unique depths, the depths corresponding to size of bird and bill length. Both age classes of chicks foraged mostly at 00-30% leg coverage but adults foraged mainly at 80-100% leg coverage. Young chicks foraged mainly at 8 mm, old chicks at 53 mm, adult females at 81 and >155 mm, and males at 4 and 100 mm. Avocets of all categories tended to forage in deeper water in the evening than during the day.

Avocets at Benton Lake had a bimodal daily foraging pattern; activity peaked in the early morning and again in the late evening. Chicks foraged during the middle of the day much more often than did adults.

The four age/sex categories of avocets utilized the five prey-capture methods (Peck, Plunge, Land/Top Peck, Bill Pursuit, Scythe) in significantly different proportions. Adults foraged mainly with peck and plunge; chicks foraged mainly with land and top peck.

Average rate of prey-capture for all birds combined throughout the day (except between 1200-1400) was approximately 25 swallows per minute. Birds foraging from 1200-1400 averaged 14 swallows per minute. Adults generally captured prey more rapidly than did chicks with all foraging methods and at all depths. Old chicks usually captured more prey per minute than young chicks. Adults caught the most prey per minute at 80-100% leg coverage and with peck and plunge. Young chicks caught the most prey per minute at 00-30% leg coverage with land/top peck. Old chicks foraged most effectively at 40-70% leg coverage and with land/top peck. In general birds in each category foraged more often at depths and with methods at which they were most successful.

Avocets at Benton Lake partition their foraging area by depth and by method of prey-capture thereby minimizing competition between adults and chicks and increasing chances of survival among young. Bill morphology changes as the chicks grow; the characteristics of the foraging niche also

consequently change. Bill dimorphisms in the adults may also increase the diversity of areas in which they may forage, thus reducing competition between the sexes.

American Avocets have evolved variable nesting activities and partition food resources by depth and by method of prey-capture between age and sex categories. These adaptations probably enhance the ability of avocets to occur in large numbers and maintain high reproductive rates in areas where they coexist with many potential competitors and predators.

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